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RESIN SECRETION IN BALSAMORRHIZA SAGITTATA

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(WITH PLATES XXVIII–XXXI AND TWO FIGURES)

Introduction

This problem was undertaken to determine the origin of the secretory tissues and the cause of resin secretion in *Balsamorrhiza sagittata*. The problem was suggested by Professor JOSEPH E. KIRKWOOD, of the State University of Montana, to whom the writer desires to express hearty thanks for valuable suggestions during the progress of the study.

Among the earliest students of secretory organs and their function was MEYEN (**13**), who stated that "these secretion organs arise from enlarged intercellular passages. One cannot consider them as mere containers, in which the secretion is laid by, but one must compare the containers with their contents to inner glands, and the surrounding walls as specialized glands." This writer proposed that the excretory cells surrounding the secretory canals prepare the balsam and then secrete it through the wall into the intercellular lumen. That the process is surrounded by a sort of mystic vagueness for MEYEN is evident from the description "wonderful" which he applied to the process. In his work on the pine MEYEN (**14**) found resin not only within the secretory passages and the surrounding cells but throughout the entire stem.

The opinions of the earliest investigators on resin formation were extremely diversified. KARSTEN, WIGAND, WIESNER, and

others of their school considered resin as a destructive slime formation secreted by the cellulose wall lining the cavity, or else a starch derivative. KARSTEN (**8**) was assured of the intimate relation between the wall and resin gum in the wall, because of the obscurity of the cells in ordinary mounts, whereas the walls became extremely clear when treated with alcohol or ether (p. 317). WIGAND (**26**) considered resins to be entirely out of the category of secretions, for "a secretion in our sense is only conceivable as a homogeneous material permeable to the cell wall." WIESNER (**24**) believed the resin masses to be a complex of resin, cellulose, granulose, tannic acid, and "carbonated alkalies," with the cellulose and granulose as intermediate products.

MUELLER (**15**) and VAN TIEGHEM (**22**) were unable to find resin in the secretory passages, believing them to be only intercellular spaces. MUELLER was probably the first to use alkannin tincture on dried tissues to test for resin (p. 390). MAYR (**12**) thought that resin might be secreted by the cells during rapid growth.

Undoubtedly the most careful and authoritative contemporary investigator of resin and the problem of its secretion is TSCHIRCH (**21**), who has given us a summation of the physiologico-chemical literature of the problem, and in addition valuable evidence contributed from his own studies. TSCHIRCH'S investigations have convinced him that resins and ethereal oils cannot diffuse through membranes which are water-permeable or water-absorbent. All such secretions, he asserts, remain where they were first laid down.

Ecological aspects

B. sagittata was first described by NUTTALL (**16**) in 1841. The plant is a very conspicuous feature of the landscape of the prairies and south hill slopes of Wyoming, western Montana, and British Columbia. Its leaves are large, auriculate, densely hairy, growing up from the permanent rootstock in April at 3500 ft. level in western Montana. The flower stocks are plentiful. The flowers are golden yellow with conspicuous heads. They begin to bloom about the middle of May and continue until July, although they reach their maximum bloom during June. Very soon after fertilization the flower parts wither, and by the time the seeds are mature in

late July the flower stocks and heads are brown and dry. The leaves remain green until the first heavy frost, when they soon assume a crackling dryness. The plant is a xerophyte, and is commonly found on the flats and upland plains, being especially abundant on the exposed south slopes of the hills. The writer has observed it frequently as high as 6000 ft. and occasionally in the subalpine areas of a still higher altitude.

Specimens of primary rootstock of graduated diameters were dug and dry cleaned and then weighed. They were re-weighed until constant air dry values had been secured. Tables I and II show the results.

TABLE I

SHOWING WATER CONTENT OF PRIMARY ROOTS COLLECTED JULY 1915; COLLECTION DESIGNATED SERIES I

Specimen	1	2	3	4	5	6
Diameter in mm	2.5	4.0	6.0	11.5	13.0	22.0
Weight in gm	0.221	1.429	1.250	2.873	4.195	6.120
Air dry weight	0.088	0.648	0.585	1.505	2.079	3.002
Percentage loss	60.69	54.65	51.45	47.60	50.44	50.95

Average loss of series, 52.63 per cent.

TABLE II

SHOWING WATER CONTENT OF PRIMARY ROOTS COLLECTED OCTOBER 1915; COLLECTION DESIGNATED SERIES II

Specimen	1	2	3	4	5
Diameter in mm	6.0	8.0	9.0	12.0	15.0
Weight in gm	2.337	2.762	3.444	4.144	6.425
Air dry weight	1.107	1.310	1.505	2.038	3.177
Percentage loss	52.60	52.60	56.30	50.80	55.70

Average loss of series, 53.60 per cent.

Tables I and II show a more uniform correspondence for water content in October than in July, although the average water content is practically the same in both series. In general one may conclude that the size of the root has no definite relation to its water content. Within the slight fluctuation the water content is directly proportional to the weight of the root. Also, the average water content is the same at these different seasons of the year.

In direct contrast to these data is the record for water content in random soil samples taken from field areas where *B. sagittata* was growing in abundance. Table III shows such sample records, with normal and air dry weights.

TABLE III

SHOWING PERCENTAGE OF WATER IN RANDOM SAMPLES OF SOIL IN WHICH *B. sagittata* GROWS

Sample	1	2	3	4	5
Weight in gm.	94.00	126.42	89.27	104.26	110.02
Air dry weight	79.11	103.64	77.55	99.12	90.03
Percentage loss	15.85	18.02	15.37	4.89	18.18

Average loss of series, 14.46 per cent.

Table III shows a fluctuation of water content in the soil entirely incommensurate with the constant water values of the rootstocks. This may be accounted for in part by the size of the soil particles, since they, too, are far from uniform, and such differences would cause both a difference in weight of soil per unit mass and a consequent difference in capillarity. The fact remains, however, that the plant, irrespective of its root size, selects a relatively constant amount of water from soils that differ noticeably in water content.

Calculations were made also to determine the percentage of resin in air dry roots and leaves. The parts selected were first weighed, then placed in pure ether in an air-tight compartment. They were left in this container for a week, during which time they were shaken frequently. This method of extraction was used after it had been ascertained that ether was the best solvent for the resin of this plant. At the end of this time the ether extract was poured off, filtered, and the ether allowed to evaporate at 20° C. until a constant weight had been secured. For roots dug in July the percentage of pure resin amounted to 3.3; for roots dug in October the percentage was 3.3; for roots dug in May, some three or four weeks after the new growth had begun, the percentage was 5.2. This shows a constant resin value during the resting period and an increased resin content for the growing period. The percentage of resin found in the leaves was 9.8. This value was found for leaves

selected and dried in the middle of May, the time of maximum growth. This resin value was found after the ethereal oil had evaporated. By the osmic acid test it was found to contain no fatty oils. An analysis of *B. terebinthacea* made by Miss HERMA T. KELLEY (**19**) indicated 9.76 per cent resin, 8.96 per cent of which was removed by chloroform and 0.80 per cent by alcohol. In addition to this there were 5.70 per cent oils, 0.42 per cent volatile oils, and 5.28 per cent of fixed oils. LLOYD (**11**) has calculated the percentage of resin for *Parthenium argentatum*, the guayule of the Mexican desert. His values are as follows:

	Per cent resin
Stump	2.46
Wood growth of 1907	1.36
Cortex of above wood	4.06
Growth of 1908	7.56
New growth of 1909 with leaves	2.70
Roots	10.80

These values were obtained from irrigated plants. WHITTELSEY (**25**) secured from 10 to 17 per cent of resin for the field plants of the same species. If the field records are taken, it is evident that by weight the resin content of *B. sagittata* is smaller than that of the related species, *B. terebinthacea*, or of *Parthenium argentatum*.

Associated with *B. sagittata* in a parasitic way is a certain fly of the Typetenid group of the family Muscidae. A complete description of this fly will appear in a separate paper now in preparation by the author. The fly is found in the receptacle of the maturing flower head, living there during the grub and pupal stages of its development. The grub is about 1.8 mm. in length by 0.15 mm. diameter, while the pupa averages 1.5 by 0.15 mm. Usually there is only one individual to the receptacle, but certain receptacles have been observed by the writer in which 5 or 6 of the parasites lived. The grub is very insidious, ordinarily boring a labyrinthine course through the upper parts of the receptacle and into the bases of the maturing seeds. The result is a twofold injury to the seed: an actual destruction of the maturing seed and a stunting of growth in the seed by intercepting the course of nutrition in the receptacle.

Two other important parasites on *B. sagittata* are a nematode and an acarinid. The former is found in the young stem bud before it appears above the ground. The worm eats its way through the bud, mostly in epidermal and cortical tissues, leaving a dry decay behind. Undoubtedly this does much to sap the vitality of the developing vegetative parts, if not entirely forestalling growth. The mite is found in the sinuses between the leaves, sucking out the juices at the bases of the new leaves. Several hundred were found at times in a single leaf bud. This parasite, too, undoubtedly causes serious damage to the plant and serves to control its abundance.

Collection and preservation of material

The material on which this study is based was collected from July to November 1915 and from April to June 1916. Certain roots, stems, and leaf buds were examined fresh, just after collection. Freehand sections were made and observations taken from water mounts. Other material was allowed to dry and was examined as such. However, the greatest part of the material was fixed in various fluids and preserved in alcohol for more detailed examination. Of this last group, material fixed in acid alcohol and preserved in 70 per cent alcohol gave the most satisfactory results. Certain seedlings germinated in the laboratory, illustrating ontogenetic growth, were fixed in Carnoy's fluid. In addition to freehand sections of the alcoholic material, sections of typical roots were made 12 μ thick in series and similar series of the stem and peduncle 8 μ thick. Sections of seedlings were cut 8 μ thick.

Various stains were tried, but the most satisfactory combination was acid fuchsin with malachite green counterstain. This combination gave an excellent contrast, since the lignified hadrome and sclerome elements, as well as suberized walls of the Casparian strip, took on a copper green against the fuchsin background. The ordinary resin stains, cupric acetate and alkannin tincture, were made use of throughout the study. The alkannin was found extremely satisfactory, since it was both specific and rapid. Osmic acid fumes (osmic anhydride) were used to test for fats. Iodine in potassium iodide was employed for starch testing. Chloriodide of zinc was

used to determine the character of the Casparian strip. Slow alcoholic penetration into inulin-testing areas caused a precipitate of this polysaccharide in the shape of sphero-crystals and rhombospheres, while a more rapid penetration caused the material to be precipitated in granular and amorphous masses. Resene was tested for *in situ* by the Mach and Salkowsky-Hesse cholesterol methods (somewhat modified to suit the immediate needs). Crystals of resene found in certain cells were positive to these tests. Similar crystals were found as a check in steam-distilled resene, dissolved in alcohol, and allowed to crystallize as the alcohol evaporated. A more complete discussion of these tests will be found under tests for resene.

The probability of error in resin tests is due in general not to a lack of a specific reagent, but to errors in location of the substance. Due to its solubility in high grades of alcohol it is not impossible that it might become translocated by alcoholic diffusion. Due to its viscous nature it might readily be dislocated in cutting sections from fresh or alcoholic material. The data of certain investigators, among whom are MUELLER (**15**) and VAN TIEGHEM (**22**), show no resin in the resin canals, while SANIO (**18**) and TSCHIRCH (**21**) were unable to find the secretion outside of the canals. Errors in technique must have been responsible for this. TSCHIRCH considered ordinary methods of technique inadequate for the elimination of the error and made use of a method adapted from MUELLER (*loc. cit.* p. 390). He dried the material at 100° C. for some time before cutting. He then stained with alkannin tincture in water (2 parts of the tincture and 5 parts of water). The former procedure allowed all volatile oils to be driven off and hardened the resin to a tough gummy consistency, so that it was not easily removed from its original position by the section cutter. The latter diluted the tincture so that the resin would not readily dissolve in the alcohol. By this method TSCHIRCH was able to demonstrate resin in the form of a dense slime in the canals of *Imperatoria Ostruthium*, *Arnica montana*, and in the leaves of *Abies pectinata* and *A. Normanni;* while the surrounding tissue, especially the secretory cells, was free from resin content. The writer has given due weight to this possible source of error, and has made many preparations from

live material, alcoholic, and dried preparations. It is only by a study of all these preparations that he feels able to present authoritative data.

Germination tests

The seeds of *B. sagittata* are ripe about the first week of July. From that time they soon become dislodged from the receptacle and fall to the ground. Between July 6 and July 15, 1915, several thousand seeds were collected and sorted into two tentative groups, those considered viable and those considered non-viable. The latter group comprised about 90 per cent of the whole. Of this non-viable group almost half were eaten at the base of the seed by the Typetenid parasite, and the remainder were small and shriveled, due to lack of nourishment. This non-viable group was discarded. Of the seeds saved, 100 choice ones were selected October 19, 1915, and weighed. Their total net weight was 1.041 gm. They were then soaked in concentrated sulphuric acid for 8 minutes, carefully rinsed in distilled water several times, and placed in a sterile moist chamber at about 30° C. during the test. The record is as follows:

SERIES I

October 19; 100 selected seeds weighed, sterilized, and set to germinate in sterile moist chamber.

November 3; one seed beginning to burst testa; hypocotyl protruding.

November 5; 3 seeds burst testa; hypocotyl of one 11 mm. long.

November 6; 13 seeds found soft and decaying; thrown out.

November 10; 11 seeds found soft and discarded.

November 11; 5 seeds germinating; 4 thrown off testa.

November 12; 12 seeds found soft and thrown out.

November 14; 8 seeds germinating.

November 17; mold developing; those seeds not yet germinating but considered sound rinsed in weak formalin solution, then thoroughly rinsed in distilled water.

November 28; 10 seeds germinating; 5 of these fixed in Carnoy's fluid, 5 transferred to cork supports in beakers of water and allowed to continue growth; all ungerminated seeds discarded.

Later, no further growth.

SERIES II

November 18; 100 seeds selected, soaked in sulphuric acid for 5 minutes, thoroughly rinsed, and set to germinate between damp filter paper in chamber as in Series I; average temperature 30° C.

November 28; mold developing; seeds rinsed in formalin solution, rinsed in distilled water, and returned to damp chamber.

December 1; culture found dry; had been dry about two hours.

No germination in this series.

SERIES III

January 25; 100 seeds selected, soaked in sulphuric acid, thoroughly rinsed in distilled water, then placed in sterile moist chamber between filter paper; distilled water supplied as needed drop by drop by siphon apparatus; temperature 25° C.

January 31; first seed bursts testa; no mold.

February 1; 5 seeds found soft and discarded.

February 10; 3 seeds germinating.

February 18; 4 seeds germinating.

February 24; 6 seeds germinating; no mold.

February 29; 8 seeds germinating; several of the remainder soft, discarded.

March 4; seeds dry for several hours; no subsequent germination.

An examination of these records shows certain interesting and significant points. A comparatively small percentage of seedlings germinated from selected seeds, due to lack of viability in apparently viable seeds and to infection during the germination tests. An extremely small percentage of seeds germinated from the total seed production. Series I gave a total of 10 per cent of seeds germinated from 100 selected seeds. Series II gave no germination, due to desiccation antecedent to expected germination. Series III gave an 8 per cent germination within the same time limit as Series I (less one day), but at a lower average temperature. The average for Series I and III is 9 per cent. A more elaborate and critical study of the germination values for *Parthenium argentatum* by KIRKWOOD (**9**, p. 39) gave 10.8 per cent for selected seeds of that species.

Since the selected seeds comprised only about one-tenth of the total seeds produced, an average of less than 1 per cent (0.9) is obtained for the ratio of seeds germinated to the total of seeds produced. Although the plant is a perennial, the severity of the winters in the exposed places where the plant grows kills out many of the rootstocks. Taking into consideration the infection of the bud and the stem by nematodes and mites, an enormous seed production would seem necessary to maintain the plant as the dominant member of the society in which it grows.

A survey of field plants was made during May 1916. Plots covering areas 300 ft. square were studied, and the number of root-stocks counted and the seedlings in those areas listed. For two such plots about 800 plants were found, equally divided between the two plots. This number comprised all plants of *B. sagittata* of all sizes and ages within the plots. An accurate idea of the distribution of the plants is seen in text fig. 1. Areas 4 ft. in radius were

FIG. 1.—Field of *Balsamorrhiza sagittata* in vicinity of Missoula, Montana, in May 1916.

closely inspected around each plant, the plants receiving numbers as the listing progressed. In plot 1, in the count of the first 100 plants, one seedling each was found for numbers 2, 3, 4, 8, and 100, no other plant having the seedling within this radius. In plot 2, for the first 100 plants counted, numbers 11, 49, 69, and 70 had one seedling each, while number 68 had two. In a second 100 in plot 2, numbers 41, 61, and 91 had one seedling each. Of those plants observed about half had borne seeds the previous year, or

about 200 per plot of 300 square ft. had been seed producers. Yet only 5 seedlings were found in the count in plot 1, only 6 in the first count in plot 2, and only 3 in the second count in plot 2, averaging 4.66 per cent, a much lower average secured than for seeds germinated indoors. It is evident from the dominance of this species in the society in which it lives that it depends largely upon the continued growth from the rootstock from year to year for maintenance of its dominance. It is not unusual for the individual rootstock to produce 100–300 seeds. This would more than replace the plant each year if the laboratory germination test were effective in the field, but the lower germination record for field plants indicated beyond a doubt that the plant could not be replaced each year by the new seedlings.

The germination in the field is comparatively late. The first of the consocies to germinate is the seed of *Lupinus ornatus*, which begins about March 1. Since *B. sagittata* does not fruit until the third or fourth year, but gives up all the time and energy the first two years to growth and food storage, it is evident that early germination is not essential to the best interests of the plant; yet the blooming rootstocks of *B. sagitatta* are in flower long before the lupine.

Of the factors determining germination, air (oxygen) is undoubtedly the most important. A test of this factor was made in a group of seeds not included in the series just cited. The same conditions prevailed in this series as in the recorded series, except that they were covered with a sterile crystallizing dish so as to exclude air. There was no germination. A careful comparison with the recorded series seems to indicate that oxygen is more necessary to prevent fungous growth than as a factor in the metabolic processes of germination per se. When seeds are once set to germinate, moisture is constantly necessary for germination, as indicated in Series II and III.

The temperature coefficient of germination is interesting. It is evident that germination is more rapid at first at 30° than at a lower temperature. However, although germination at 25° is slower, that appears to be a more advantageous condition, since at that point a maximum growth of the plant is effected for a

minimum growth of fungus. Undoubtedly under field conditions the temperature is constantly less than 25° C., except for a short time during the warm afternoons. In fact, practically any night during the germination period (middle of April to middle of May) a freezing temperature may be recorded.

Certain seeds which actually germinated or commenced to germinate had been injured in the region of the root cap or even in the region of the meristem of the root. This was the cause of a decreased vitality in the entire plant and was often the occasion for rapid bacterial infection. This injury was originally due to the Typetenid parasite in the receptacle of the flower head. Such an injury must be a source of constant decay to germinating seeds in wet ground.

Structure

ROOT.—In the developing seedling of *B. sagittata* at a very early stage, a day or so after the seedling begins to break through the testa, certain cells begin to differentiate into protoxylem. These occur at four angles of the root section, forming a tetragon, giving rise to the tetrarch structure of the primary root. At first these spiral tubes develop singly, but may later be followed by one or two others centripetally at each angle of the tetragon (fig. 7). As might be expected from their later origin, these secondary spiral vessels are somewhat larger than the elementary vessels. At this earliest differentiation of protoxylem there are no indications of protophloem from procambium. Very soon, however, such differentiation begins midway and slightly centrifugal to the line joining the first quartet of protoxylem elements (fig. 8). The procambium cells in this region divide tangentially, with apparent irregularity, developing protophloem externally and at the same time intermediate protoxylem internally. Such growth is represented in figs. 9 and 10. These periclinal divisions continue until 4 or 5 concentric rows of phloem are formed and until the xylem almost completely envelops the axial plate. At this time the axial plate is still composed of undifferentiated tissue quite irregular in contour, strikingly similar to the stem pith of the plant. The leptome strands are limited externally by the undulating endodermis, con-

spicuous now (fig. 10) by anticlinal suberization. The appearance of the thickenings is knotlike or looplike along the radial walls. The endodermis, unlike that of *Parthenium argentatum*, contains no starch grains such as commonly occur in higher plants.

The secondary xylem contains not only well defined spiral vessels and tracheids, but vessels of intermediate type. For instance, in fig. 11, *c* and *d* with bifurcating spiral reinforcements are not far removed from *a*, the true spiral type, while *e* more nearly approaches the eyelet type so characteristic of the tracheids.

In the dicotyledons the usual type of axial structure is parenchymatous; but such is not the case in *B. sagittata*, for there the wood elements soon work centripetally, crowding against the original plate cells. The latter become sclerified, so that the plate becomes a solid disk of vessels and sclerome. Such sclerification begins before radial suberization of the endodermis and considerably earlier than resin duct formation. The centripetal crowding with the addition of the new xylem elements increases the actual size of the region within the cambial ring.

The suberized endodermis serves a twofold purpose. The suberization thickens the walls and allows the endodermis to act as a supporting girdle, and, in addition, acts as an impervious barrier against an external translocation of food material. RUSSOW (**17**) has described two types of suberization of endodermis, that in which the radial and one tangential walls are thickened (his "C" type), and that in which the entire wall is thickened on all sides (his "O" type). HABERLANDT (**6**, p. 372) suggests that such distinction is not of great mechanical importance, since variations may occur within the same genus, such as *Carex*, *Smilax*, etc. Although the "C" type is the most usual in *B. sagittata*, there also occurs the "O" type, and in woody secondary roots a thickening which may be designated as an "H" type (fig. 12). In the primary root of 5 mm. or over, the suberized endodermis is interrupted in regions between resin canals by phloem strands which cross into the cortex in these regions, leaving open an avenue for translocation of materials in these special places (fig. 13, *ph*). The origin and development of the resin canals will be discussed later in this paper.

In the older rootstocks of two or more years' growth three regions may be distinguished, a basal primary root, a median swollen region, and two or more branched root growths above the swelling. From the upper reaches of these proximal root branches arise the aerial portions of the plant system. The lowest root region is characterized by a single row of resin canals and an axial stele, while both of the other parts have two concentric rows of resin canals (fig. 14). Cross rays connect these longitudinal canals at frequent intervals. These old rootstocks are further characterized by lysigenous splitting of the now functionless rays, so that the wood is split apart in almost every ray region (fig. 15, l_1, l_2). This cracking is probably caused by tension in the wood areas and a shrinking of the cells in the near vicinity.

The subsidiary root system of *B. sagittata* varies from the main system in that it is diarch in type. The protoxylem first becomes differentiated as two groups at opposite poles, with evidence of protophloem developing intermediately (fig. 16). By the time the suberization of the endodermis occurs, intermediate wood elements have developed and the axial plate is well sclerified (fig. 17). It is not until considerably later that the resin ducts arise (fig. 18).

The root of the plant has a rather large wood area compared with the extra-cambial portion of the root. Table IV shows that it is practically a ratio of two to one through all stages of secondary thickening.

TABLE IV

Number	Diameter of root	Ratio
1	2 mm.	2:1
2	3.5	2:1
3	4.5	2:1
4	12	8:5
5	12	2:1

This excess of wood tissue may be accounted for by the area occupied by the rays extending between the wood elements. In no. 5, with two rows of resin canals, lysigenous cracks in the ray region occupy about half of the wood area.

While the tracheids conform to the usual type for Compositae and the phloem cells show no unusual characteristics, certain

features of the stone cells deserve special consideration. These cells are found principally in the hypodermal region and give a hardness to the cortex, which makes untreated material difficult to section. They take on a vivid green with the malachite stain. They are somewhat larger than the surrounding cortical parenchyma, due to their thickenings. In surface view they present a polygonal appearance, with bluntly rounded corners (fig. 19, *a–d*). A view at the edge of the cell shows circular pores which enlarge and approach one another as they invade the center of the cell. The center of the cell is an irregular space devoid of the sclerified material, usually filled with ordinary parenchyma cell protoplasm. This content fails to react to starch, oil, or resin tests. As the canals of the cells near the lumen, they anastomose in pairs or triplets, giving an appearance as shown in fig. 19, *d*. The cells have at least one transverse diameter longer than the longitudinal (compare fig. 19, *c* with *d*). This same type of stone cells also occurs in the axial plate of old woody roots (both primary and secondary), and in the wood of subsequent formation, although it is never found in phloem regions. In the latter tissues it is supplanted by bast strands (fig. 13). The stone cells usually occur in groups of five or six.

STEM AND PEDUNCLE.—The hypocotyledonary stem contains the tetrarch arrangement, as shown in fig. 20. The phloem is exarch and the xylem endarch, with protoxylem innermost. As progress is made up the stem, the meristematic region where the bud resides is approached, containing secondary stem, leaf, and flower structure. At this place the four main strands each give off two anastomosing bundle strands to the bud, while the major portion of the bundle strands continues into the cotyledonary collar (fig. 21). Slightly above the section diagrammed in this figure certain changes occur in the bundle strands. These are best illustrated by a comparison of the section shown in fig. 22 with fig. 24, a diagram of the course of the bundles, seen longitudinally. Between levels *cc* and *dd* strands are given off from *w* and *x*, which unite above *dd* to form a median strand *p*. Coincidentally laterals from *y* and *z* form the median strand *s*. Similarly above the section *dd*, *x* and *y*, *z* and *w*, give off subsidiary strands which anastomose in pairs to form respectively

r and *t*. A section taken between *cc* and *dd* might show all the way from 4 to 12 strands, depending entirely upon the exact level of the section, and a section taken above *dd* might show from 6 to 8 for the same reason. Slight variations in the origin of coincident laterals due to unequal nourishment would be shown in an odd number of traces. Returning to figs. 20–23, diagram 22 occurs about the level *dd*. Laterals from *w* and *x* have been given off to form *p*, but have not yet anastomosed. A lateral from *z* to form *s* has been separated from the parent bundle, but its mate from *y* is still intact within *y*. Meanwhile traces from *x* and *z* have already arisen for the formation of *r* and *t*, although their mates are still within the main bundles *w* and *y*. Hence the actual derivations are atypical in location, although the end results are the same, that is, 4 median strands (*p*, *r*, *s*, *t*) derived from uniting limbs of the 4 original bundles (*w*, *x*, *y*, *z*). The section in fig. 23 shows a level above *dd*, where laterals are being derived from *t* and *w*, *y* and *s*, *y* and *r*, to form strands of tertiary rank, with laterals from *w* and *p* not yet derived. Already *x* and *z* have been broken up by a twofold bifurcation.

Certain atypical traces were found in the study of the tissues of *B. sagittata* at this period in its development. In one series of sections the laterals from *x* and *p* received a trace from below. Further observation showed this trace to end blindly at a lower level. In another series the lateral from *z* to *s* was found to give back certain strands to *z* before the lateral united with its mate from *y*. In such cases transverse sections alone would be difficult to use in tracing such bundle anatomy. In older stems and in the peduncle 8–24 traces are derived, dependent on the amount of conduction required in these parts.

LEAF.—The leaf type of a seedling is defined with reference to the number of traces in the blade which appear as separate entities at the origin of the leaf blade from the petiole. In his studies on some 50 seedlings of representative groups of Compositae LEE (10) has chosen *Silphium perfoliatum* as the type for Heliantheae, to which tribe *B. sagittata* belongs. The general superficial appearance of *S. perfoliatum* and the plant under consideration is very similar. Both seedlings are large and hardy, with no secondary

roots up to this period of development. In writing about the bundle strands of this type LEE states as follows:

> As usual in this order the single vascular bundle at the apex of the cotyledon first divides into 3, after which, in correspondence with the large size of the cotyledons, each main strand gives off a large number of smaller bundles. At a lower level, these begin to re-fuse with the larger strands, and at the base of each cotyledon only 5 vascular strands remain, a large median one and two smaller laterals on either side. In the pronounced cotyledonary tube the extreme lateral and smallest bundles fuse with the corresponding bundles from the other cotyledon, and the composite structure produced, after decreasing in size, moves around and joins on to one of the remaining strands. At a still lower level in the cotyledonary tube, the remaining lateral bundles fuse in pairs, so that 4 canal vascular strands enter the hypocotyl.

Upon examination of seedlings of *B. sagittata* it is evident that neither the cotyledons (figs. 22–24) nor the first true leaf (fig. 6) possess bundle traces exactly corresponding to the type for the Heliantheae. There are considerably more than 5 strands for the region above the origin of the blade (fig. 23), but at a level just below the cotyledons in the cotyledonary collar (fig. 24, level *dd*) only 6 strands are found, although in certain sections even below this level (fig. 22) a greater number is indicated, due to peculiarities of transverse anastomoses. Even the true leaf (fig. 6) shows only 3 bundle strands at the origin of the blade from the petiole. It may be said, therefore, that for *B. sagittata* we have a type of bundle anatomy of somewhat fewer strands than for *Silphium perfoliatum*. With these exceptions it has a general resemblance to the tetrarch anatomy of the Heliantheae.

RESINIFEROUS DUCTS.—A root of a young seedling with cotyledons not yet outspread shows clearly the resin secretion from the protoxylem outward through the cortex. There are large drops of resin at the time the endodermis begins to take on suberized thickenings, yet at this stage no resin ducts have formed. Not until the seedling is some 60 days old do the ducts begin to form in the root. The development, although surely determined beforehand, does not occur until after resin formation. The method of development is schizogenous. First a periclinal division occurs in the endodermal cell opposite a group of tracheids. This is followed by an anticlinal division, so that 4 cells arise from the original endodermal cell

(fig. 26). A lumen develops in the midst of the 4 cells, which canal becomes the cavity for resin secretion. Usually the 4 cells now divide obliquely with new planes of division parallel to the walls of the duct, so that the duct becomes lined with 2 layers of cells (figs. 27, 28). A consequent cleavage at right angles to the walls of the duct gives rise to 8 cells immediately lining the duct (figs. 29, 30). This ring of ducts in the cortex, just outside the endodermis, is the usual complement of ducts for the root. As the root grows, however, room is made between the older ducts and new ones are formed. The resin ducts of the root are continuous from the basal region to the junction of the root with the stem. These ducts are somewhat more undulatory than are the tracheids. At times there is evidence of the fusion of 2 ducts, but this is merely due to a breaking down of internal processes from the cells surrounding the lumen rather than an anastomosis.

An examination of seedlings of 2 mm. or over shows in the hypocotyl 2 concentric series of resin canals, the outer series continuous down through the entire root system, and the inner merely potential in the younger seedlings. The 2 series are connected by radial canals between the longitudinal lumina of the series and by transverse canals between consecutive longitudinal canals of the same ring (fig. 31). Moreover, the inner series is capable of ventral extension in roots of one year or over, so that they extend down and around the median enlargement of the root. At this place they all anastomose in a common center (fig. 14).

This type of concentric rings with radial anastomoses corresponds to observations made by CALVERT and BOODLE (**2**) for *Manihot Glaziovii*, but is the reverse of LLOYD'S (**11**) observations on *Parthenium argentatum*.

The ducts in the stem consist of 2 separate systems. These systems have similar origin and structure, but different location. One series is found in the pith opposite the wood of the bundles, while the other series occurs in the cortex opposite the interfascicular region, almost within the interstices between the phloem of the bundles (fig. 25). These ducts arise somewhat earlier than those of the root and apparently are not connected with those of the root system in any way. They are continuous throughout the

entire stem, although they are intercepted in certain regions by processes from the lining cells, as shown in fig. 35. The origin of both these systems in the stem is schizogenous and follows the same sequence of development as outlined for the duct system of the root. HOLM (**7**), working on the anatomy of *Solidago odora* (pp. 252–254), quotes VAN TIEGHEM as saying that resin ducts have only been observed in the cortex (primary) "in certain species of *Solidago*, including *Kleinia;* otherwise these ducts are frequent in the pith and in the secondary tissues." The two series of ducts in the stem of *B. sagittata* indicate a composite type of duct anatomy, in that they supply a duct system in the primary cortex, hitherto observed only in species of *Solidago*, and in addition supply the usual system of the pith. These ducts, too, are subsequent to resin formation in the stem.

The resin ducts of the leaf are merely upward prolongations of the stem systems, corresponding to the bundle trace relationships already indicated. For each bundle in the leaf there are two canals, one occurring on the upper side of the leaf and the other one on the lower side opposite the hadrome elements. DEBARY (**4**) gave a very complete table of the duct systems as far as they had been worked out in his day, VILLUEMIN (**23**) has studied it in certain species, and COL (**3**) has added to the knowledge of the subject, but a thorough revision of the literature needs to be made in order to bring the knowledge up to date.

Since VAN TIEGHEM prepared his schematic outline for types of resin duct distribution in the stems of Compositae, at least two new types have been observed, namely, the *Solidago* type described by HOLM (**7**) and the type represented by *B. sagittata*, described in this paper. For this reason it is necessary to reconstruct VAN TIEGHEM'S scheme to include the more recent observations.

OUTLINE KEY TO SECRETORY PASSAGES IN STEMS OF COMPOSITAE TYPES

I. Stem containing passages within bundle sheath
  A. Passages confined entirely to medullary region . . . . . *Ageratum conyzoides*
  B. Passages both within and without bundle strands
    1. Only one medullary passage for each leaf trace bundle
      a) One medullary and one cortical passage

i. Both passages opposite the bundle ..... *Solidago limonifolia*
ii. Medullary passage opposite the bundle, but cortical passage in the interstices between bundles .. *Balsamorrhiza sagittata*
b) One medullary and several cortical passages *Serratula centauroides*
2. A group of medullary passages for each group of cortical ones
a) Group compact ..... *Carduus pycnocephalus*
b) Groups in curved series ..... *Helianthus tuberosus*

II. Passages wholly without bundle strands
A. Passages external; not walled in on inner side by endodermis or pericycle ..... *Solidago odora*
B. Wall of passages partially formed by endodermis or pericycle
1. Passages single, not in groups
a) One passage in middle of outer margin of each main leaf trace ..... *Senecio vulgaris*
b) One passage in middle of outer margin of each main leaf trace; in addition one passage for each single bundle in such united trace ..... *Aster* sp.
c) One passage on each side close to phloem of each main bundle trace ..... *Tagetes patula*
2. Passages in groups
a) Three to five passages opposite outer margin of phloem and of main bundle ..... *Silybum marianum*

Physiology of resin secretion

Numerous theories have been proposed to explain the origin of resin and the methods of resin secretion. Among the more important sources conceived as a basis for resin formation may be named the following: starch, cellulose, tannic acid, phloroglucin, a hypothetical glucoside, terpene, and even chlorophyll. As diversified as are these substances, there may be at least superficial reasons for relating resin to any one of them. However, only a deeper analysis of the problem, following out a particular coincidence of resin and one of these materials, will show whether the relationship is a genetic one or not. Evidence is here presented showing certain relationships of the resin secreted by *B. sagittata*.

The resin of this plant appears as a viscous exudation, especially from newly dug roots. It is a light lemon color in smaller quantities, but in larger amounts (ether extraction) it appears a golden yellow. It contains a small amount of essential oil, but gives no

tests for fatty oils. In the roots of young plants (two years or less) it is found mostly in the outer ring of canals, while in old roots it occurs in the two concentric rings of canals, together with the radial anastomoses.

As has previously been mentioned, the ordinary resin tests are cupric acetate and alkannin tincture. The acetate requires several days and imparts a brilliant emerald to the resin. The alkannin causes the resin to take on a brilliant crimson in a very short time. The resin may be distinguished from oils of a fatty nature by the osmic anhydride test. The alkannin is much more soluble in the higher grades of alcohol, but such a high concentration of the solvent is not desirable, since it also acts as a ready solvent for the resin.

The TSCHIRCH test for resin, modified from MUELLER, was used by TSCHIRCH for demonstrating that resin was present in the lumina of canals of *Imperatorium Ostruthium*, *Arnica montana*, *Abies pectinata*, and *A. Normanni*. In fact, TSCHIRCH noted a layer of slime among all schizogenously formed canals. The writer has made use of this technique for testing resin in *B. sagittata* and *Parthenium argentatum*. These preparations show resin in the canals, as described by TSCHIRCH, but in addition demonstrate resin in the newly formed xylem, an abundance of it in rays and inner regions of cortex, including the cells immediately surrounding the canals, and *great masses of resin in the cambium*. Such dry preparations demonstrate resin in the identical locations as the aqueous mounts from fresh material and alcoholic material. In this wise an accurate check has been secured on the demonstration mounts.

An analysis was then made to discover the approximate relation of resin to other organic materials. Resins are classified according to their reactions to four kinds of tests: resino-tannol, resene, resiniferous oil, and resinic acid tests.

The resino-tannols are those resiniferous materials which react to tannin tests. For example, when ferric chloride is added to a solution of resino-tannol, iron tannate is formed as a precipitate. Other reagents used to test this relationship are potassium bichromate, lead acetate, potassium hydrate in alcoholic solution, and nitric acid. Should any of these reagents give a positive test, an exceedingly difficult problem would then confront the investigator.

Since tannin is not a single compound, but a convenient name for a related group of compounds, separate tests of the entire group would then be necessary. Moreover, as TSCHIRCH has pointed out (*loc. cit.* 1142), such a test would not necessarily prove a genetic relationship, since tannin might be merely a by-product and not its source.

Samples of the resin (ether extraction) from *B. sagittata* were submitted to the resino-tannol tests. All samples gave negative test except the one where nitric acid was used as the reagent, in which case the test was atypical. This test was so positive, however, that it served to indicate a possible relationship of another nature. Two or three drops of the pure resin were placed in concentrated nitric acid. The resin globules became dark brown, with a violent evolution of nitric oxide in the course of two minutes, accompanied by the formation of a cellulose membrane across the top of the solution. When heated, this membrane burned with a warm yellow flame and heavy smoke, leaving a black char. The odor was like that of burning celluloid. The test was then repeated with resin dissolved in 95 per cent alcohol. The reaction was delayed, not taking place for 5 minutes, but was accompanied by a more violent evolution of the gas. When the test was repeated with the resin dissolved in absolute alcohol, the test reaction did not take place for 6 minutes, and was even more violent than on either of the previous occasions. Such a reaction would indicate a relationship to cellulose or other carbohydrate.

The second group of resins are called resenes. They are the ones showing kinship to the terpenes and the fatty aldehydes. The modified cholesterol tests are applied to these substances. Two of the more common and specific ones are the Salkowsky-Hesse and Mach reactions. In the Salkowsky-Hesse test 0.002–0.003 gm. of the resin is placed in 3 cc. of chloroform and shaken with 3 cc. of concentrated sulphuric acid. The chloroform solution is then evaporated in a porcelain dish and the color of the residue noted. The color differs for various known resenes, from orange through lavender to blue, but is always a constant index for a particular resene. Substances that are not resenes do not give such color tests. In the Mach tests 0.003 gm. of the resin is placed in 1 cc.

of concentrated hydrochloric acid and evaporated in a porcelain dish and the residue washed. If the test is positive, the residue is usually blood orange or red. Both the Salkowsky-Hesse and the Mach tests were applied to the July and October resin of the *Balsamorrhiza*. The results were negative.

As previously described, the fatty oil test is made with osmic acid. A slide with a thin smear of the resin is inverted over a solution of the acid or of the crystals. The fumes of the reagent cause fatty substances to blacken. When the osmic anhydride was applied to resin of *B. sagittata*, no positive test was secured, even after prolonged application.

If resin gives an acid reaction to litmus or requires several portions of one-tenth normal sodium hydrate to neutralize, it is said to be a resinic acid. Such acids unite with ammonium hydrate and the hydrates of the alkali metals to form unstable resinic esters. A great number of these resinic acids are known, although their chemical formulae have been worked out only empirically. Certain of these acids have been distinguished by the type of ester formed with ammonium hydrate. For example, the group to which pimar acid belongs builds a very beautiful acid ammonium salt, while the group to which abietic acid belongs forms with ammonium hydrate a non-crystalline gelatinous emulsion (see TSCHIRCH, *loc. cit.* 519). The resin of *B. sagittata* gives a very decided acid test. It combines with ammonium hydrate, potassium hydrate, and sodium hydrate to form resinic esters. Moreover, the ammonium ester is an emulsoid.

The evidence gained from these tests shows that the resin of *B. sagittata* is a member of the resinic acid group, giving an ester with ammonium hydrate similar to that of abietic acid, and that it has certain relationships to carbohydrates in that it forms a nitrocellulose when reacted upon by nitric acid.

It was found that by a distillation of the resinic acid, either from the gross plant structure or from ether extracted resin, in the presence of steam, an entirely new product was formed. The substance had a tendency to crystallize upon cooling below 25°, and gave off a very characteristic pungent odor, sweetish, but very irritating to the mucous membrane. The substance was white, opaque, and

crystallized out of water in a very elaborate form, simulating frost crystals. Later it was found that it crystallized as long monoclines out of alcohol or ether. The two resene tests were applied to this substance, with positive results in both cases.

SALKOWSKY-HESSE TEST

Sulphuric acid solution after shaking: golden yellow.

Chloroform solution before evaporation: pale yellow, nearly colorless.

Residue after evaporation of chloroform in porcelain dish: first, bright yellow; later, rich dark brown; red brown; ending in deep violet.

No fluorescence.

MACH TEST

Color of residue from evaporation of alcoholic solution of resin with hydrochloric acid and ferric chloride: dark red.

This resene is saturated, failing to absorb iodine, but is weakly acid.

These positive tests, together with the general physical properties of the substance, were proof that the material under analysis was a resene, a type of fatty aldehyde. It was further discovered that all of the resinic acid was converted into resene in the process of steam distillation.

Two preparations of resene from steam distillation of spring roots were made during August 1916. One of these was placed in a glass-stoppered bottle and the other in a loosely corked vial. An examination after 6 months showed that the former preparation was in the original crystalline state, while the latter had been converted into a lemon-colored resin, and had completely lost its crystalline structure. This fact supports the view that the resene had been converted into resinic acid by an oxidative process, such as holds true for terpenes in general. This process follows the natural method expected in the plant tissues, and is the reverse of the reduction process in the presence of steam.

The discovery that resene is derived from resinic acid gave rise to the inquiry as to whether resene might not be found in the *Balsamorrhiza* plant; in short, whether there might not be a genetic connection between the two substances in the plant itself. The following methods were carried out in this inquiry: modified resene tests *en bloc* and modified Mach tests applied microchemically.

In the tests *en bloc* equal portions of *Balsamorrhiza* roots (alcoholic preservation of August material) and sprouting stem buds (fresh March material) were each placed in 5 cc. of chloroform and left for two days. The plant tissues were then removed and 5 cc. of sulphuric acid added, according to the Salkowsky-Hesse method, and the mixture thoroughly shaken. The results are given in table V.

TABLE V

	August root	March bud
Sulphuric acid solution	Pale tan	Colorless
Chloroform solution	Colorless	Colorless
Residue from evaporation	Colorless	Lavender to violet
Iridescence	None	Marked between solutions

The Mach test (modified) was used on sections of rapidly growing stem buds, just previously placed in 85 per cent alcohol. Sections of this material were cut in 95 per cent alcohol; 1 cc. of this alcohol, 1 cc. of ferric chloride, and 1 cc. of hydrochloric acid were mixed and the sections transferred to this mixture on a depression slide. The slide was then gently heated until the mixture was reduced to about 1 cc. Even from gross inspection a typical Mach test was produced in the vascular tissues. Examination under low power of the microscope showed reactions in the following places: heavy stain in the cambium and rays (identical with regions testing heavily for resin in fall tissues); specially marked test against walls of endodermis facing cortex; all through cortex and pith to more or less degree. In the heavily testing regions masses of monoclinic crystals were found, deeply impregnated with the stain from surrounding crystals that had dissolved (fig. 37). This same test was applied to roots of the August collection, preserved in 60 per cent alcohol. The results of the test were negative. This very specimen block had been used previously for resin tests and had yielded a decided resin test in the vascular and conductive areas.

These two tests, the Salkowsky-Hesse and Mach, modified to meet the needs of the material under investigation, applied to *Balsamorrhiza* material, showed a negative test for fall roots and

a uniquely strong positive test for the spring bud region. In fact, a comparison of the former test with the present one would indicate a much higher percentage of the resene in the spring bud than was necessary for a test reaction. Moreover, the Mach test both checked up the results obtained in the Salkowsky-Hesse reaction and gave the precise location of the resene in the growing bud.

A final test to check up the previous determinations consisted in placing some of the material of the fall collection and the spring collection in absolute alcohol-ether, half and half, for a period of two days, then allowing the filtered solution to evaporate. No crystals were found from a careful examination of the fall roots, yet an abundance of crystals of the monoclinic type were secured from the spring stem material.

The evidence secured from these reactions for tissues of *B. sagittata* shows (1) that resene is found in the growing plant tissues, in the meristem and conductive areas; (2) that resene is found in the same region in spring tissues where resinic acid is found in the fall tissues; and (3) that resinic acid areas in fall tissues test negatively for resene.

In the middle of May roots dug about May 1 were tested for percentage of ether extract. Such data are recorded in the ecological section of this paper. This material shows both resene and resinic acid present in tissues at this particular time of the year, when the leaves had been well developed and metabolic processes were near the zenith point.

When tests were made on various parts of the plant to discover whether a Mach test could be secured, the test was negative. These tests were made on stem and root tissue and on cotyledons and embryo within the seed coat. Later certain crystals were noted in the connective and storage tissues of the plant, spheroidal in shape, with rays arising from an eccentric umbo. The crystals were observed in material which had been preserved in alcohol *en bloc*. These crystals did not occur in fresh aqueous mounts nor in fresh material sectioned and mounted in alcohol. The type of the crystal was such and its reaction to reagents such as to establish

it as the crystallized inulin, a colloidal polysaccharide. In ordinary growing tissues these crystals are deposited in a viscous lemon-yellow mass, but in alcohol they undergo certain changes in shape. In readily permeable tissues they are laid down as granular masses, but where there is slow alcoholic penetration they are laid down as sphero-crystals. Such crystals are well illustrated and their location shown in fig. 36 (*si*). They are found in connective tissue, especially in the rays and in the inner cortex. In this same specimen the canals are filled with resin. The semiviscous, semigranular resene is well brought out in fig. 16, the section of a very young subsidiary root without secondary thickenings yet developed. In fig. 17, the section of a subsidiary root further developed, is shown in the more permeable outer region of the cortex the semiviscous, semigranular inulin, while the sphero-crystals are found in the inner cortex, not so permeable to alcohol.

Other observations on the growing stem buds showed the following relationships. Young etiolated stem buds showed no inulin, while green stem buds were filled with inulin. Such observations are proof that the result of the photosynthetic process in *B. sagittata* is inulin. Such a substitute for starch is found in the related Compositae, *Helianthus annuus*, *Inula Helenium*, and for roots of *Dahlia* spp.

As the microchemical tests progressed, evidence became stronger that a genetic relationship existed progressively in turn between each two of the three products found in *Balsamorrhiza*, namely, inulin, resene, and resinic acid. The hypothesis built up on this evidence may be stated thus:

Inulin < resene < resinic acid; in other words, inulin, a polysaccharide, formed in the plant in the process of photosynthesis, by a process of polymerization is changed to resene, and by reduction the resene is altered to resinic acid, a waste product of the plant. The direct evidence supporting this view may well be summarized at this point: (1) etiolated stem buds contain neither inulin nor resene, while green leaves test for both coincidentally; (2) resene and resinic acid are found in the stem and root at the same time; resene more frequently occurs in conductive tissue and

resinic acid in ducts and canals; (3) resene is derived from resinic acid in the presence of steam; (4) resene is converted into resinic acid in the presence of oxygen.

A suggestion of the effects of resinic ester and resene on the vegetative growth of *B. sagittata*, and in consequence an idea of the physiological nature of the products, is shown by the effect of these substances on the living protoplasm. Although this plant is not listed among the poisonous plants of the western stock ranges along with the death camas (*Zygadenus venenosus*), the loco weeds (*Aragallus* and *Astragalus* spp.), the larkspurs and the lupine (*Lupinus ornatus*), it is the common belief of stockmen that the root and stem of *B. sagittata* often cause stock poisoning, especially among sheep. Certain experimental proof of this toxic property of the resinic esters and the resene of this plant will be presented.

A neutral potassium resinate was prepared from titration with a saturated solution of potassium hydrate and an alcoholic solution of the resinic acid. The alcohol was allowed to evaporate and the ester dissolved in water to make a saturated solution. A few drops of this solution were introduced into a watchglass containing filaments of *Chara* in 10 cc. of tap water. Such a dilute solution of the ester was not sufficient to effect any osmotic changes in any appreciable way. Observations were made in the following manner.

A filament of *Chara* had previously been singled out and the rate of flow of the protoplasm under low power of the microscope noted. A convenient distance was chosen on a blank paper at the side of the microscope, and by means of a camera attachment the time for this distance flow was then taken to ascertain the average time flow. Such an average in this case was found to be 20 seconds, with a maximum at 22 and a minimum at 18 seconds. A final normal reading was taken at 9:14 A.M. and the specified amount of the ester introduced. Five minutes later the time flow was 30 seconds; 6 minutes later, 27 seconds; 7 minutes later, 25 seconds; 8 minutes later, 23 seconds; 13 minutes later, 23 seconds; 15 minutes later, 20 seconds; and at 10:38 A.M., 19 seconds. This shows an immediate effect in the time flow and a rather rapid recovery. When a double dose of the solution, that is, 6 drops of the

saturated solution to 10 cc. of water, was used, the following data were secured:

12:40–12:58 P.M.	Time flow 20 seconds
12:59 ester introduced	
1:00	25
1:01	30
1:02	30
2:03	35
2:04	35
4:18	40
4:22	30
4:25	32
4:26	33
4:30	30
5:00	60
5:04	60
9:00 A.M. following, death of the filament, but with no plasmolysis	

Check experiments on a new filament with the same toxic doses were used, with similar results.

TRUE (**20**), working on *Lupinus albus*, found for inorganic acids that the H ion produced the greater toxic effect on the vitality than the Na ion of the sodium salt. The same was correspondingly true for organic acids, with the toxicity proportional to the dissociation of the H ion. It may be noted in passing that the resinic acid would probably be more toxic than the potassium salt.

In the process of steam distillation of the resene condensation at 10° C. is not complete. Unless the apparatus is inclosed in a hood with a good vent, the room soon becomes permeated with the volatile resene. It has a characteristically sweetish odor, very terebinthine in nature. During a period of 3–4 hours the writer was in the immediate vicinity of a resene still, with the room temperature at 22° C. and the condenser at 10°. Certain pains developed under the eyes with sharp, shooting pains in the occipital region. Also a dull pain developed in the spinal cord, mostly in the lumbar region. Within a short time a high fever arose (102–104° F.), alternating with chills. At times, as the chills abated, the blood coursed through the head, seemingly laden with fire. A tickling sensation

was produced in the respiratory tract, centering in the bronchi, giving rise to coughing which seemed almost to split the head. This condition continued for almost 36 hours, at the end of which time the fever began to abate and the acute pains to leave. The irritation of the lungs and bronchi continued for more than a week before it was relieved.

A similar test was made, except that the windows were wide open and a strong breeze blew the vapors away from the writer. No ill effects were observed. Again, when the apparatus was thoroughly hooded, no harmful effects were felt.

In steam distillation, where water and resene distil and condense simultaneously, the resene collects on top of the distilled water. It was found, however, that a fine grade of filter paper does not free the filtrate of the resene product, evidently due to a colloidal suspension of the resene in the water. When exposed to the air and allowed to evaporate for some time, some of the suspensoid is precipitated in crystal form. The toxic effect of this colloidal suspensoid of resene is brought out by the effect on the protoplasmic flow of *Chara*.

Resene was distilled from fall roots of *B. sagittata* and allowed to condense at 10° C. along with water. This water was filtered and the filtrate allowed to act on *Chara* sp. It tested tannin free. The normal time flow for a unit distance was found to be 10, 10, 10, 10, 10, 10, etc. The *Chara* was then transferred to this colloidal suspension, in parts one of the suspension to nine of water free from the suspensoid. Observations on the effect of the resene on the protoplasmic flow were made for 90 minutes. The observations are recorded in table VI.

A study of the data shows a marked lowering of the vitality immediately upon the introduction of the resene, followed by increased activity of the protoplasm. The lowering of the protoplasmic flow occurred almost rhythmically, followed by an alternate rhythmic increase in vitality. This continued until the final decrease in flow, with death ensuing. The amount introduced was much less than that required for an appreciable exosmosis (text fig. 2).

The writer recognizes that a correct quantitative measurement of the toxicity of resene and resinic esters is desirable, and has under

way such a test, together with a physiological standardization of the products.

TABLE VI

RECORD OF EFFECT OF COLLOIDAL SOLUTION OF RESENE FROM *B. sagittata* ON PROTOPLASMIC FLOW OF *Chara* SP. THROUGH UNIT DISTANCE OF 0.465 MM.

Time	Time flow	Time	Time flow	Time	Time flow
7:15 P.M.	10	7:41 P.M.	18	8:09 P.M.	12
7:16	10	7:42	No record	8:10	13
7:17	10	7:43	13	8:11	14
7:18	10	7:44	12	8:12	15
7:19	10	7:45	8	8:13	14
7:20*		7:46	8	8:14	No record
7:21*		7:47	10	8:15	"
7:22*		7:48	10	8:16	13
7:23	15	7:49	12	8:17	13
7:24	15	7:50	12	8:18	13
7:25	16	7:51	14	8:19	19
7:26	14	7:52	18	8:20	20
7:27		7:53	13	8:21	15
7:28	10	7:54	18	8:22	14
7:29	8	7:55	18	8:23	14
7:30	6	7:56	22	8:24	No record
7:31	12	7:57	23	8:25	"
7:32	15	7:58	28	8:27	18
7:33	12	7:59	22	8:28	No record
7:34	10	8:00	18	8:29	14
7:34.5	8	8:01	13	8:30	11
7:35	15	8:02	12	8:31	14
7:35.5	20	8:03	12	8:32	12
7:36	17	8:04	12	8.33	15
7:37	16	8:05	14	8:34	24
7:38	14	8:06	11	8:35	∞ with death
7:39	14	8:07	No record		
7:40	18	8:08	16		

*Resene introduced here.

Discussion

A survey of the study of resin secretion makes it evident that the problem can be considered logically only in the light of the threefold evidence, the ecological, the anatomical, and the physiological. The assertion of TSCHIRCH (*loc. cit.* p. 1145) that "we shall assuredly not arrive at a conclusion by anatomico-microchemical" investigations is only a half truth. All phases of the problem must be carefully weighed in order to understand the problem. In this evidence the anatomico-microchemical data surely have their place.

The writer does not claim that the particular solution of resin secretion for *B. sagittata* is a complete solution for resin secretion

in all plants. However, it suggests a method of attack to be followed in working out other problems of a similar nature and scope.

The problem of resin secretion in *B. sagittata* is one limited to the field of an acid resin, non-tannin testing. For this type of resin, perhaps by far the most common, theories have been advanced

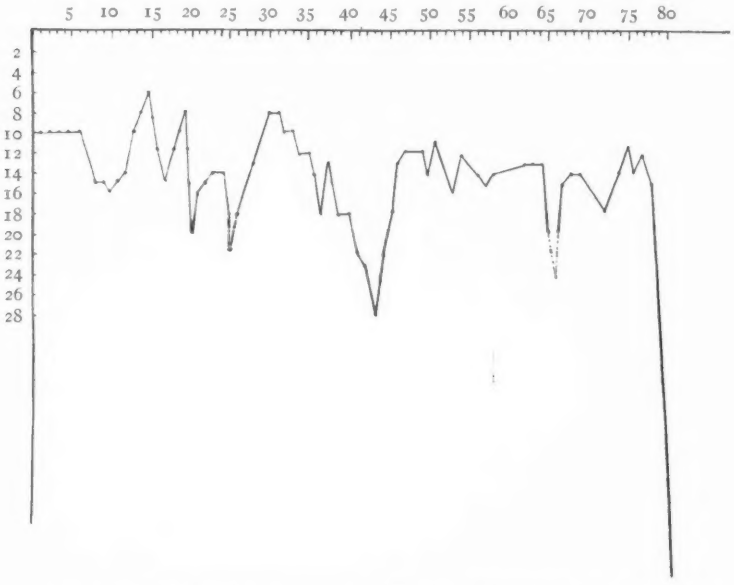

FIG. 2.—Coordinate plot, representing effect of balsamoresene on protoplasmic activity of *Chara* sp; the ordinates represent time flow and abscissas sequence of time.

advocating the origin from carbohydrates on the one hand, and the origin from terpenes on the other. Foremost of those advocating the former theory was WIESNER (**24**). He assumed that resins are derived from carbohydrates, specifically starch, by polymerization and reduction. As he knew, this fails to account for resin in the pine family, where there is a maximum production of resin but very little starch formation. WIESNER explained this on the basis that gallo-tannic acids operated to produce the change in this family.

Recently FRANKFORTER (5), working from the biochemical angle, has criticized WIESNER's theory on the ground that it is unreasonable to suppose a complex starch molecule would be formed and then broken down into the terpene and resene radical. The criticism is not well founded, because it fails to consider the fundamental function of resin secretion. In other words, this criticism evades the anatomico-physiological viewpoint which TSCHIRCH claimed could never solve the problem; but in evading this point of view the entire meaning of resin secretion is overlooked.

The theory of resin formation from terpenes is supported both by theoretical and actual evidence. Such a theory was postulated by BAEYER (1), who obtained several resins by oxidation of fatty aldehydes, although these resins were unlike any found in nature.

The evidence presented from a biochemical study of *B. sagittata* shows (1) the presence of a resinic acid, with reaction similar to that for abietic acid; (2) production of the fatty aldehyde, *balsamoresene*, by steam distillation of the resinic acid and the formation of the resinic acid from resene in the presence of oxygen; and (3) a strong test for inulin, a polysaccharide, in photosynthetic and conductive areas, in conjunction with balsamoresene. This evidence, added to the comparative studies, warrants the assumption that *balsamoresinic acid is derived from balsamoresene*, which, in turn, is derived from inulin by polymerization.

Although the evidence already presented in the physiological section is the most convincing, yet that secured from the ecological data and anatomical observations brings the problem to a clearer focus. HABERLANDT (*loc. cit.* p. 525), referring to the coincident bundle traces and secretory canals, concludes that "the reason for the frequent association of secretory passages with leptome strands and other vascular tissues is, therefore, in all probability, an ecological one." Furthermore, "the substances contained in these passages are often of such a kind as to be capable of affording 'chemical protection' against noxious animals; hence small assailants which have penetrated into the interior of an organ will be more or less effectually discouraged from attacking the conductive strands, the continuity of which is so vital to the well-being of the

plant, if the latter are protected by a series of secretory ducts (or excretory sacs)."

A criticism of this theory lies in the fact that it fails to comprehend the origin of resin per se, and tries to explain its reason for existence *ab exteriore*. The ecological evidence from *B. sagittata* would discourage any such reason for resin secretion. As has been described, diptera, acarinids, and nematodes parasitize the growing and reproductive parts of the plant. The fly nymph lays the eggs between the parts of the flower head, where the grub hatches and worms its way through the tissue, irrespective of resin canals, effectually limiting the source of nourishment of the ripening seeds and causing a high percentage of non-viability. The mites suck the juices of the conductive tissue, especially at the bases of the new stems and petioles, where there is an abundance of resin in the tissues. The nematodes bore into the conductive tissues of the leaf and bud and cause a withering and decay right in the resin secreting areas.

Another ecological reason assigned for resin secretion is its protection against mechanical injury to cortex. It is based on the ground that such injured places are often covered by a resin covering. Undoubtedly this is often true, but it must be considered a secondary function, not at all the fundamental reason for resin secretion.

The fundamental underlying reason for resin secretion lies in the essential toxic nature of the resin to the plant itself. The resin is a by-product, formed in the metabolic activities of the plant. It is harmful to the plant, as judged from its effects on other organic tissues and from the storage of the product within special tubes or canals in the endodermal region, near to the place of greatest activity and growth. Since these resene and resinic acid products are toxic, they may be used as a guard against mechanical and parasitic injury. They may or may not be effective in such capacity.

Moreover, the anatomical observations verify this hypothesis. The balsamoresinic acid and the balsamoresene develop in cambium and other meristematic regions. They are carried outward by the rays and phloem strands until they reach the resin canals, where

they are laid down. Such seems to be the significance of the penetration of the phloem strands into the cortical areas through the Casparian strip (fig. 13).

Much emphasis has been placed by TSCHIRCH (*loc. cit.* p. 1118) on the non-permeability of resinic acid through cell walls. This author contends that resin is laid down where it is formed. Yet in an alkaline medium, such as is frequently if not always found in growing tissues, an unstable resin ester would be formed, undoubtedly capable of penetrating cell walls. Then, too, the fact remains that a considerable part of the resin forms in the meristem and is transferred to the canals, else it would never get to the canals. Such a transfer could be accomplished in the form of a temporary ester. On the other hand, the microchemical observations show that the larger amount of the product is transferred as balsamoresene and changed to the acid in the vicinity of the cells immediately surrounding the canals or in the canals themselves. There is even evidence to support the view that inulin may be changed into resene and later into resinic acid in the vicinity of the canals. In fact, such a change is actually shown in progress in fig. 36. There seems to be no specific way for the translocation of the by-products to the resin ducts. It may be accomplished by a temporary ester formation, or by the translocation in the form of balsamoresene, and later changed into resinic acid, and it may be centrifugally distributed as a fractional depolymer of inulin, and consequently changed to resene and resinic acid near the canals. Any one of these means would satisfy the needs of a translocation in a dialyzable form.

Summary

1. *Balsamorrhiza sagittata* is the dominant member of its habitat in the inter-mountain region. The plant depends largely upon growth of the rootstock for propagation. It does not produce flowers until the third or fourth season. A hardy rootstock accounts for its dominance, since the viability of the seeds is small, due to parasitic infection.

2. The radicle has the tetrarch type of development. The resin canals of the root arise in two concentric rows above and

including the hardy mid-rootstock, with radial canals between the longitudinal canals of the two series. Only the outer of the two series of canals is found in the lowest portion of the rootstock and the subsidiary roots. A twofold series of canals is found in the stem and leaves, an outer series in the sinuses of the cortex opposite the interfascicular regions, and a second inner series in the pith opposite the hadrome elements. The root canals and the stem canals arise as two separate systems and remain distinct. The resin canals do not arise until long after resin is formed in the meristem.

3. *Balsamoresene* and *balsamoresinic* acid are formed in *B. sagittata* from *inulin*, probably by polymerization and reduction. The resene and resinic acid are essentially toxic in nature. The resene is the immediate substance from which resinic acid is formed. The secretory process is dependent on physiological activity in the meristem of the plant, in which inulin is used in anabolism and resene and resinic acid are derived as waste products in the plant. The resinic acid and resene are transferred to the secretory canals, where they are stored.

4. To summarize, the study of *B. sagittata*, with especial emphasis to the meaning of resin secretion, has developed certain facts regarding the purpose of resin secretion. In the growth of the plant a polysaccharide, inulin, produced during photosynthesis, is broken down, causing a by-product, balsamoresene, to be produced. This resene is changed to resinic acid. On account of the probable toxic nature of the resene and resinic acid to the plant, they are translocated to schizogenously formed ducts of endodermal origin, where they are stored as resinic acid.

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EXPLANATION OF PLATES XXVIII–XXXI

FIGS. 1–6.—Successive stages in germination of seeds of *Balsamorrhiza sagittata:* fig. 1, seed coat bursting, with hypocotyl protruding, 15 days' growth; figs. 2–5, stages from 20 to 40 days' growth; fig. 6, stage showing 60 days' growth; note type of venation in plumule; figs. 1–5, ×1.5; fig. 6, ×1.

FIGS. 7–10.—Successive stages in development of bundle anatomy of seedlings: fig. 7, formation of protoxylem, other tissues yet undifferentiated; fig. 8, protoxylem (*px*) well defined, rapid differentiation of procambium (*pc*) in region where protophloem originates; fig. 9, rapid division of cambium to form secondary xylem elements (*mx*) and phloem (*ph*); fig. 10, suberization of endodermis (*en*) beginning, secondary xylem, the metaxylem, well differentiated; ×112.

FIG. 11.—Gradation of tracheids from spiral protoxylem to true eyelet type of metaxylem; taken in region of fig. 10; ×150.

FIG. 12.—Detail of suberized walls in region of endodermis, defining "H" type of thickening: *ex*, toward cortex; *in*, toward leptome.

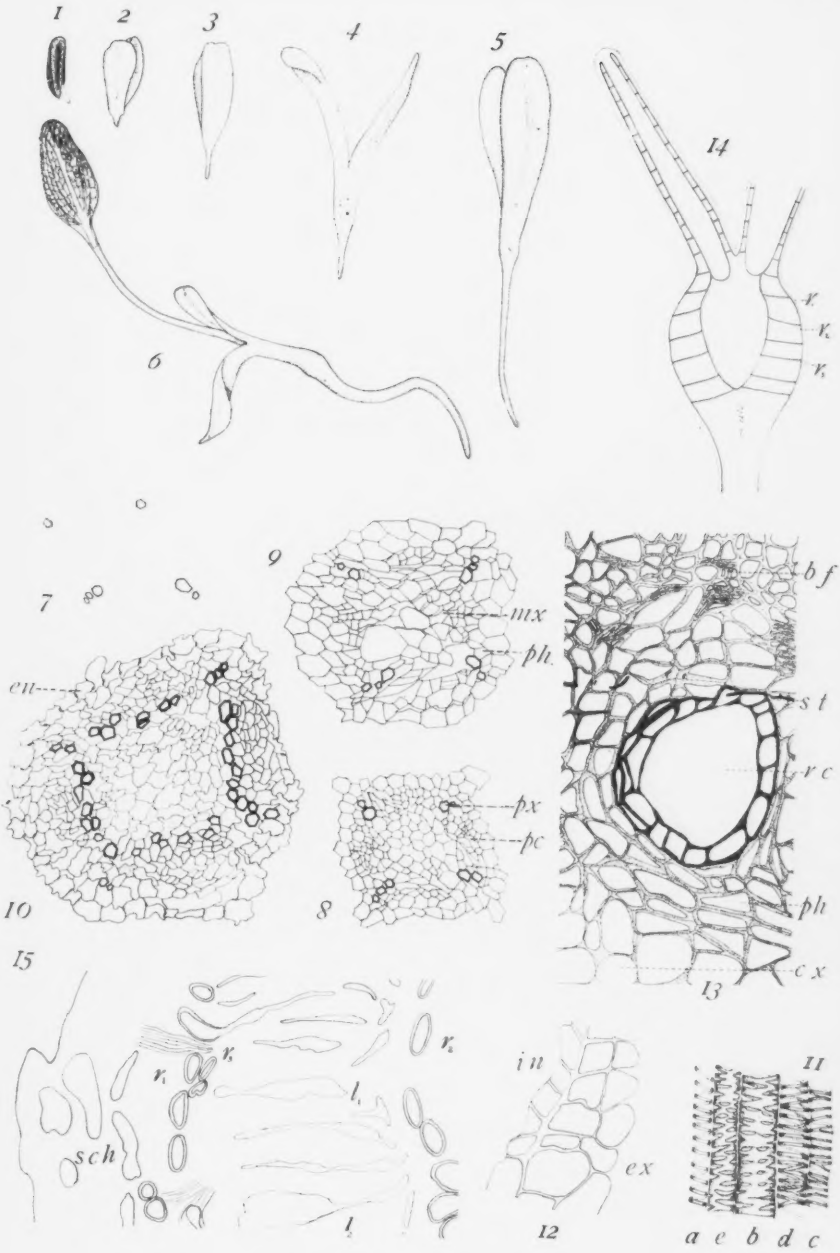
FIG. 13.—Section through 10 mm. root, illustrating passage of phloem strands through endodermis into cortex in region of canals: *ph*, phloem cells; *rc*, resin canals; *bf*, strands of bast fibers; *cx*, cells of cortex; *st*, suberized thickening of endodermis; ×150.

FIG. 14.—Diagram of resin canals in longitudinal section through stout rootstock and root branches: r_1, outer series of canals; r_2, inner series of canals; r_3, anastomosing radial connections; note inner series ends in stele just above tap root; ×0.75.

FIG. 15.—Transverse section through old root: r_1, outer series of canals; r_2, inner series of canals; r_3, radial connections; *sch*, sclerome groups; l_1, l_2, lysigenous splittings of rays; ×150.

FIG. 16.—Section through young subsidiary root with stele yet unsclerified, showing bundle anatomy: *px*, protoxylem; *cx*, cortex; *hyp*, hypodermis; *e*, epidermis; note deposits of inulin in granular masses; type of root readily permeable to alcohol; ×150.

FIG. 17.—Section through subsidiary root with moderate thickenings; note suberization of endodermis, rapid division of cambium, metaxylem ele-



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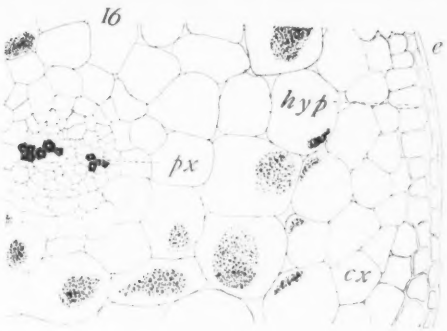

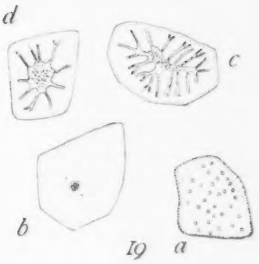

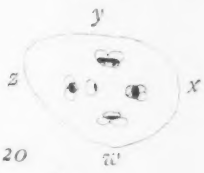

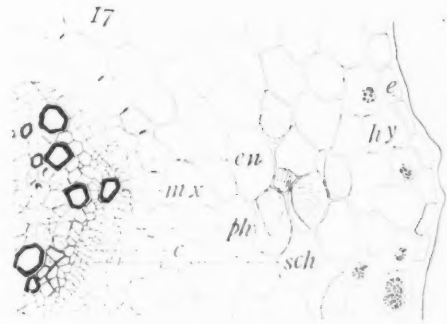

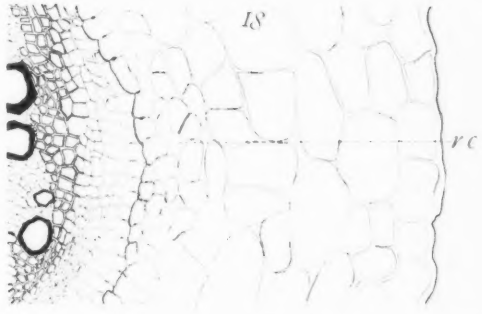

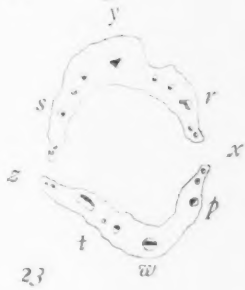

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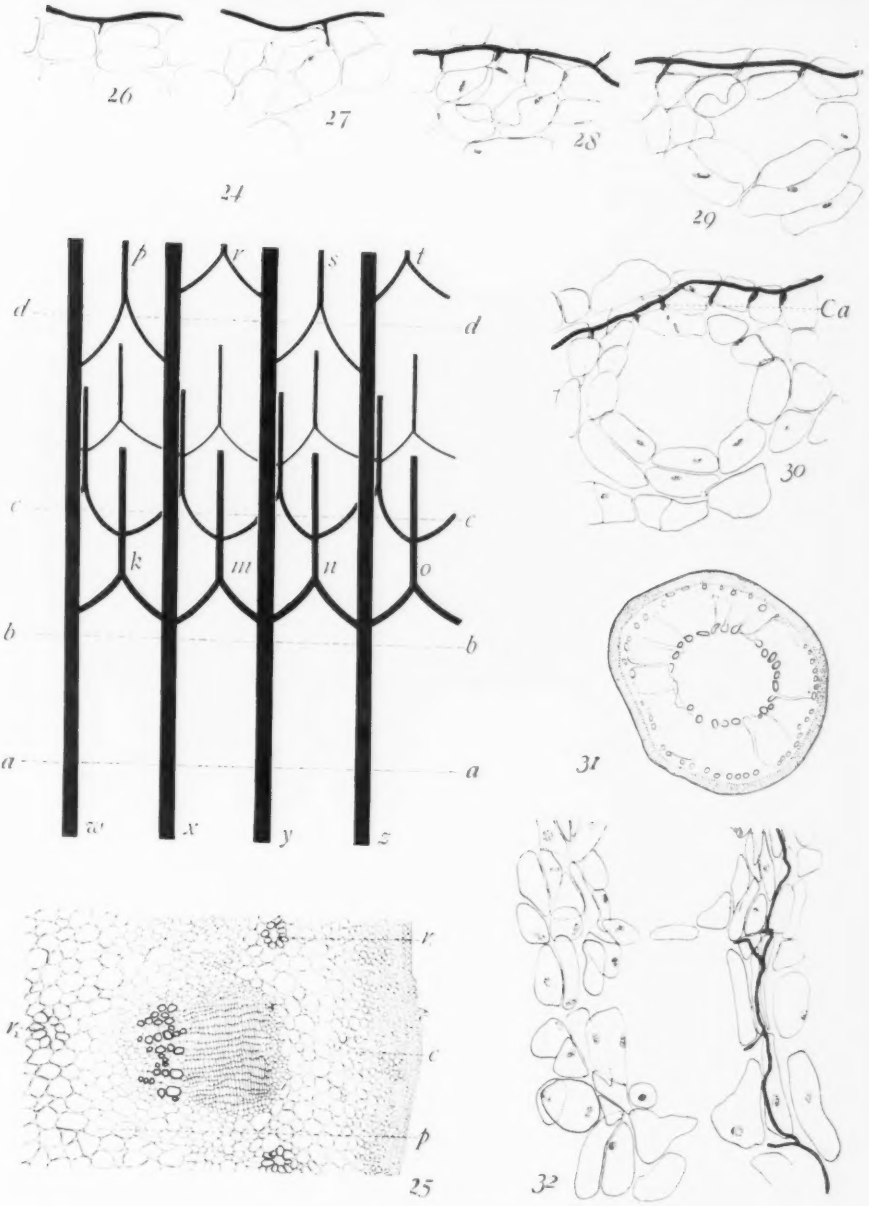

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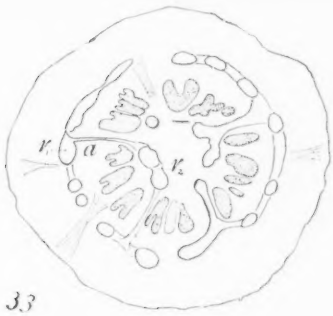

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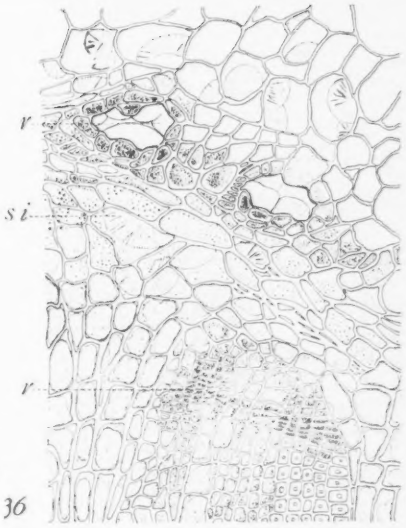

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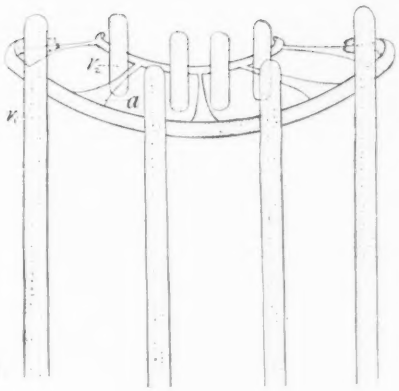

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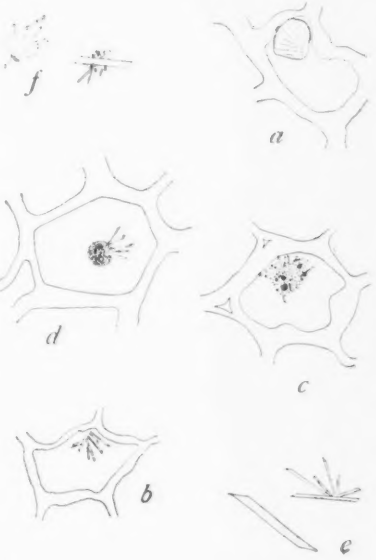

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ments, and sclerified stele; inulin deposits in outer cortex granular; in inner cortex, sphero-crystals; *mx*, metaxylem; *ph*, phloem; *c*, cambium; *sch*, sclerome; *en*, endodermis; *hy*, hypodermis; *e*, epidermis; ×150.

FIG. 18.—Section through old subsidiary root, showing formation of resin canals in region of endodermis: *rc*, resin canals; ×150.

FIG. 19.—Detail of sections of stone cells: *a*, section at edge of cell showing unsclerified pores; *b*, border of internal opening; *c*, *d*, through center of cells; *a*, *b*, *d*, longitudinal sections; *c*, transverse sections; ×300.

FIGS. 20–23.—Sections through critical levels of a 2 mm. seedling: fig. 20, region of hypocotyl; fig. 21, lower cotyledonary collar; fig. 22, upper cotyledonary collar; fig. 23, lower reaches of cotyledons; *w*, *x*, *y*, *z*, primary bundle traces in hypocotyl; *p*, *r*, *s*, *t*, secondary bundles of cotyledonary collar; white areas in bundles, phloem; black areas, xylem; dotted areas, metaxylem; ×60.

FIG. 24.—Longitudinal diagram of bundle traces in region of hypocotyl and lower epicotyl, reduced to one plane: *k*, *m*, *n*, *o*, primary traces of epicotyl; other designations as in figs. 20–23.

FIG. 25.—Transverse section through peduncle: *p*, pith; *c*, cortex; r_1, resin canals of outer series; r_2, resin canals of inner series; ×150.

FIGS. 26–30.—Cross-sections of resin canals of root at various stages of development: fig. 26, first periclinal division of initial endodermal cell; fig. 27, first oblique division; figs. 28, 29, progressive stages in formation; fig. 30, fully developed canal; *Ca*, Casparian thickening; ×150.

FIG. 31.—Transverse section of old root (4 or 5 years), showing two series of canals and radial anastomoses; ×1.

FIG. 32.—Longitudinal radial section of fully developed canal; ×150.

FIG. 33.—Transverse section of young seedling in hypocotyledonary region, showing radial anastomoses of two series of resin canals in root system: r_1, outer series; r_2, inner series; *a*, radial canals.

FIG. 34.—Schematic diagram from sections, illustrating extent and connections of resin canals of 5 mm. seedling, in region of hypocotyl: r_1, outer series of canals; r_2, inner series of canals; *a*, radial canals.

FIG. 35.—Section through origin of resin canals of stem: *a*, initial canal cell in process of division; *b*, cells dividing a second time; *c*, *d*, subsequent divisions to form canals; ×300.

FIG. 36.—Section of 3-year-old root, stained to show distribution of inulin and resin: *si*, sphero-crystals of inulin; *r*, *r*, resin deposits.

FIG. 37.—Detailed sketch of inulin, resene, and resinic acid: *a–d*, within pith cell of stem; *e*, *f*, deposited from evaporation of alcoholic solution; *a*, crystal of inulin; *b*, crystals of resene within cell; *c*, *d*, resene crystals imbedded in resin masses; *e*, detail of resene crystal; *f*, resene crystal imbedded in resin masses; ×150.

DISTINGUISHING CHARACTERS OF NORTH AMERICAN SYCAMORE WOODS

WARREN D. BRUSH

(WITH PLATES XXXII–XXXVIII AND THREE FIGURES)

Native sycamores[1]

Four out of the five known species of sycamores (*Platanus*) are natives of North America. One of these is found in the eastern United States, one in the southwest, one in the Pacific Coast region, and one in Mexico. The only species in the Old World inhabits central and southern Europe and southwestern Asia. The North American species are the common sycamore (*P. occidentalis* L.), California sycamore (*P. racemosa* Nutt.), Arizona sycamore (*P. Wrightii* S. Wats.), and the Mexican sycamore or alamo (*P. Lindeniana* Mart. and Gal.). The oriental plane tree (*P. orientalis* L.) is perhaps the most widely known as well as one of the largest trees in the temperate climate and is frequently planted for shade in streets and parks.

Gross structure

The only sycamores considered in this paper are the three species native to the United States: the eastern or common, the California, and the Arizona sycamores. The woods of these native sycamores so closely resemble each other in general appearance that

[1] The name sycamore rightly belongs to a fig tree (*Ficus sycomorus* L.), a native of Asia Minor. Sycamore is a combination of two Greek words, *sykon*, a fig, and *moron*, a mulberry. The leaves of this oriental fig tree resemble those of a mulberry. In Australia this name is applied also to *Panax elegans* F. and M. and *Sterculia lurida* F. and M. In France the name *faux sycomore* is given to the China-tree (*Melia Azedarach* L.). The name is popularly applied in this country to sycamore maple (*Acer pseudo-platanus* L.), because of a general resemblance of the leaves. Plane tree is the generally accepted name for the oriental *Platanus orientalis*, and it has been applied to the North American *P. occidentalis* from early times. The names applied locally, however, are buttonball, buttonwood, cottonwood, and water beech. Buttonball is a suitable name because it has not been applied to any other tree, and it is descriptive of the fruit. Sycamore is the accepted trade name and the one most widely used.

the elements which serve as distinguishing characters must be magnified, to some extent at least, for positive identification. The chief distinguishing characters of the sycamore woods are the color of the sapwood and heartwood and the size of the pith rays. The average weight[2] and hardness of these woods differ very little, and hence they cannot be depended upon as distinguishing characters. Specific gravity and the weight per cu. ft. are shown in table I.

TABLE I

Species	Specific gravity	Weight in lbs. per cubic foot
Platanus occidentalis	0.5678	35.39
Platanus Wrightii	0.4736	29.51
Platanus racemosa	0.4880	30.41

SAPWOOD AND HEARTWOOD

While the sapwood and heartwood usually do not show distinct limits, they are easily distinguishable from one another by their color. The sapwood of the eastern sycamore is light brown, and the heartwood has a decidedly reddish tinge; the sapwood of California and Arizona sycamores is a yellowish white, while the heartwood is somewhat darker and only slightly tinged with red. In all species the sapwood occupies only a thin zone. Both the color and thickness of the sapwood and heartwood, however, are very variable, depending probably to some extent upon the age, climate, soil conditions, and the general health of the tree. Trees growing in low or moderately wet soil usually develop thicker sapwood than those found on higher well drained ground. As a rule the eastern species has a thicker sapwood than the western ones.

ANNUAL RINGS OF GROWTH

Annual rings of growth in all three species (pls. XXXII–XXXIV, *ew* and *lw*) are clearly visible to the unaided eye. Each ring is defined from the next layer by a more or less distinct

[2] The Hardwood Manufacturers' Association has determined the weight of eastern sycamore lumber to be 3200 pounds per 1000 board feet. The weight per board foot of the western species has not been listed.

tangential line made up of several rows of radially flattened wood fibers which mark the outer boundary of the late wood. The early wood of the next annual ring lies immediately outside of this dense tissue, and it begins with a more or less continuous row of pores. The portion of the ring formed in the beginning of the year's growth is thus considerably more porous than that produced at the end of the season. The pores are slightly less numerous and smaller in diameter in the late wood than in the early wood, but they are so nearly uniform in size throughout the annual rings of growth that with the unaided eye they do not materially assist in defining the inner and outer boundaries of growth rings.

The annual rings do not differ in the three sycamores except that in the eastern species they are less clearly defined than in the other two. The width of these annual layers of growth varies considerably. The annual diameter increment of the eastern species for trees of about 90 years of age and growing under average soil and site conditions is approximately 0.2 in. per year. On an average the western species grow much more slowly.

PITH RAYS

The numerous broad pith rays constitute the most striking character of sycamore wood; they are conspicuous (pl. XXXII, *pr*) both in the transverse and radial sections. In the distinctness of its pith rays sycamore woods have a general resemblance to beech, the large pith rays of the latter, however, being less numerous. The rays of sycamore wood are very conspicuous in quarter-sawed boards, giving the cut surface a "silver grain" effect similar to quarter-sawed oak. In tangential or "bastard cut" boards the pith rays are least conspicuous, although clearly visible to the unaided eye. With the hand magnifier they appear as numerous and evenly distributed, short, vertical lines.

As stated, the size of the pith rays is one of the chief distinguishing characters of the sycamore woods. In gross structure (as seen with the hand lens) the rays are decidedly larger and usually darker in the common sycamore than in the other two species.

Minute structure

The pith rays are the only reliable means for identifying the woods of the sycamores. As viewed in the tangential section, the pith rays are broadest horizontally in the common sycamore and narrowest in the California species; the rays are lowest vertically in the common sycamore and highest in the California species. The rays of the Arizona sycamore are intermediate in character. These characters can readily be seen under the microscope.

VESSELS

The wood of the sycamores is diffuse porous, that is, the pores or vessels are of approximately the same size and more or less evenly distributed throughout the annual ring of growth. They are often grouped, and together they constitute about one-half of the transverse area between the pith rays. In outline these pores are irregular and may be oval, elliptical, or nearly round; the sides in contact with other vessels are usually much flattened. The vessels first formed in the spring are usually compressed tangentially. Average diameters were computed from 50 measurements on each of the 3 species, and show very little variance (table II).

TABLE II

AVERAGE, MAXIMUM, AND MINIMUM DIAMETER OF VESSEL SEGMENTS OF THE THREE SPECIES

Species	Average	Maximum	Minimum
Platanus occidentalis	0.083 mm.	0.101 mm.	0.063 mm.
Platanus Wrightii	0.076	0.094	0.039
Platanus racemosa	0.073	0.093	0.062

The vessels are thin-walled and are composed of numerous short segments placed end to end. The upper and lower ends of these segments are usually slanting, the oblique end always facing the pith rays. In tangential or radial section these segments are readily measured under the microscope; table III gives averages computed from 25 measurements on each species.

TABLE III

AVERAGE, MAXIMUM, AND MINIMUM LENGTHS OF VESSEL SEGMENTS OF THE THREE SPECIES

Species	Average	Maximum	Minimum
Platanus occidentalis	0.786 mm.	0.889 mm.	0.718 mm.
Platanus Wrightii	0.549	0.727	0.390
Platanus racemosa	0.677	0.749	0.608

WOOD FIBERS

These elements form the ground mass of sycamore wood, and their walls are usually much thicker than those of other wood elements. The fiber length does not differ very much for the three species. They are shortest in *Platanus racemosa* and longest in *P. Wrightii*, but the difference is so slight that it cannot be depended upon as a reliable distinguishing character. Table IV gives the average lengths of 100 measurements on each species.

TABLE IV

AVERAGE, MAXIMUM, AND MINIMUM LENGTHS OF FIBERS OF THE THREE SPECIES

Species	Average	Maximum	Minimum
Platanus occidentalis	1.63 mm.	2.02 mm.	1.39 mm.
Platanus Wrightii	1.69	2.02	1.47
Platanus racemosa	1.55	1.93	1.26

TRACHEIDS

The tracheids of sycamore wood (pls. XXXII–XXXIV, *t*, and fig. 1, *E*) are found usually adjacent to vessels. These elements, together with the wood parenchyma fibers, form more or less continuous irregular lines throughout the masses of wood fibers, from which they may be distinguished by their thin walls. Tracheids take an intermediate position in respect to size and form between vessels and wood fibers, and in sycamore wood they often possess characters belonging to either one or the other of these two very dissimilar kinds of elements. About midway between these two extreme forms (the vessel and the fiber) is the more or less fixed form,

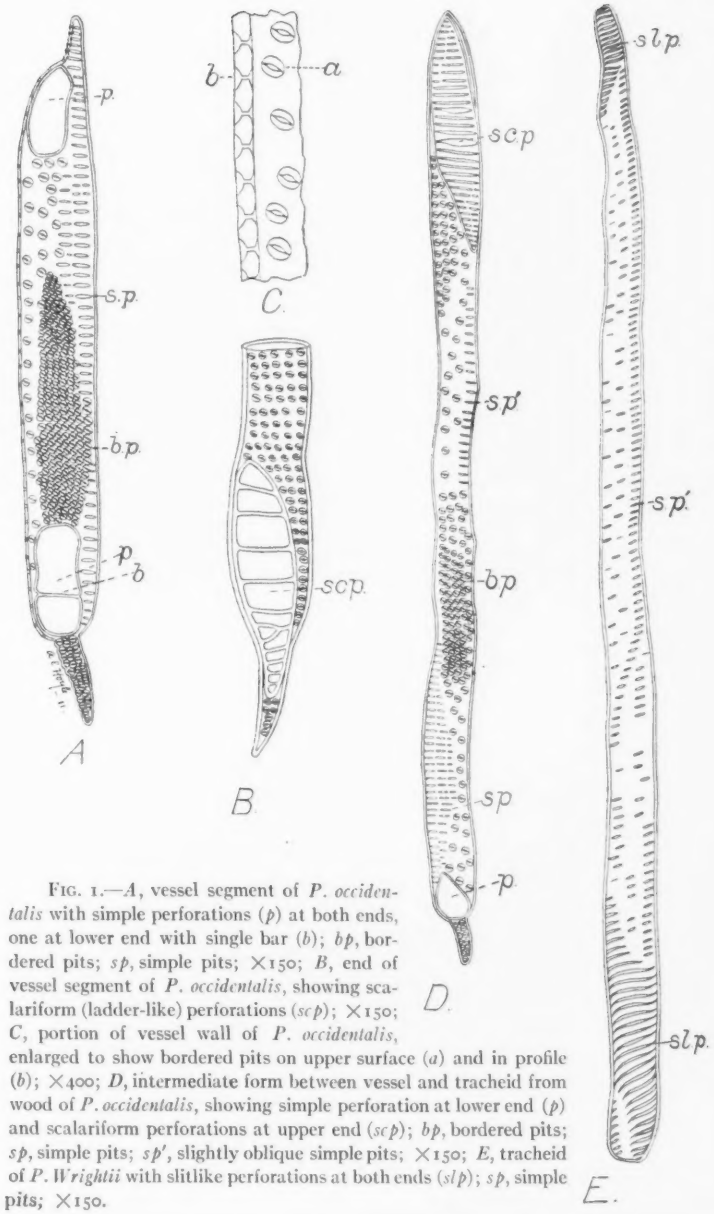

FIG. 1.—*A*, vessel segment of *P. occidentalis* with simple perforations (*p*) at both ends, one at lower end with single bar (*b*); *bp*, bordered pits; *sp*, simple pits; ×150; *B*, end of vessel segment of *P. occidentalis*, showing scalariform (ladder-like) perforations (*scp*); ×150; *C*, portion of vessel wall of *P. occidentalis*, enlarged to show bordered pits on upper surface (*a*) and in profile (*b*); ×400; *D*, intermediate form between vessel and tracheid from wood of *P. occidentalis*, showing simple perforation at lower end (*p*) and scalariform perforations at upper end (*scp*); *bp*, bordered pits; *sp*, simple pits; *sp'*, slightly oblique simple pits; ×150; *E*, tracheid of *P. Wrightii* with slitlike perforations at both ends (*slp*); *sp*, simple pits; ×150.

the "typical tracheid" or "true tracheid." This form, which occurs in the wood of practically all of the broadleaf trees, is analogous to the tracheid of the conifers. From the primitive tracheid form there seem to have developed throughout the broadleaf tree species two highly specialized forms, vessel and wood fiber. In the genus *Platanus* the general term "tracheid" must be made to include all transitional forms between the typical tracheid and the vessel on the one side, and between the typical tracheid and the wood fiber on the other side.

The typical tracheid is moderately thin-walled, has oblique simple pits, and the perforations at the ends are slitlike (fig. 1, *E*). The tracheid forms between the typical tracheid and the vessel possess, in addition to the oblique simple pits, rows of oblique bordered pits and transverse simple pits, both of which forms occur in the walls of vessels (fig. 1, *A* and *D*, *bp* and *sp*); and the perforations at the ends may be simple, either with or without bars, or scalariform, as in vessels; or the perforation may be a transitional form between the scalariform as found in vessels and the slitlike perforations found in true tracheids (fig. 1, *D*, *sp*). The tracheid forms between the typical tracheid and the wood fiber are somewhat slender, pointed at both ends, and thick-walled, and possess the vertical bordered pits of wood fibers in addition to the oblique simple pits belonging to tracheids. They often have also small transverse slits like those in the ends of true tracheids (fig. 2, *D*, *slp*). These tracheid forms (or tracheids) of sycamore wood, therefore, although extremely variable, may be defined as moderately thin-walled, elongated elements with slightly oblique elliptical or slitlike simple pits and slitlike perforations at the ends. They may also possess those pits common to either vessels or wood fibers, and the perforation at the ends may be simple, scalariform, or slitlike, these types often grading into each other.[3] The average tracheid is 1.3 mm. in length and about 0.04 mm. in diameter.

[3] A study of such transitional forms as are found in the wood of the sycamores is of great value to the student in wood structure, in that it shows the relationship of the elements to each other and assists in their classification and in the recognition of the essential features belonging to each class.

WOOD PARENCHYMA FIBERS

Wood parenchyma fibers, used for the storage of food materials, are usually less than half the length of the wood fibers, are moderately thin-walled, and composed of a number of individual cells. In sycamore woods wood parenchyma fibers occur only in the neighborhood of vessels and pith rays, from which they obtain their food supply. Each fiber consists of 1–8 oblong or cubical cells. Two forms of wood parenchyma fibers may be distinguished in sycamore wood. The fibers of the first form communicate directly with the vessels and have large transverse simple pits (fig. 2, *A*). The fibers of the second form communicate with one another and with those of the first form, but they do not communicate directly with the vessels; these have dotlike bordered pits (fig. 2, *B*).

INTERMEDIATE FIBERS

Intermediate fibers, although very similar to wood fibers, also serve for food storage. They are slightly thinner-walled and shorter than the latter and possess many small oval oblique bordered pits. They may be distinguished from the wood fibers, among which they are sparsely scattered, by the starch contained in them. They are intermediate in form and function between wood parenchyma fibers and wood fibers; hence the term "intermediate fiber."

PITH RAYS

The three species of sycamore woods may be distinguished from each other by the pith rays. The rays of common sycamore are much broader in tangential section (pl. XXXV, *pr*) than those of the other two species. They have an average width of 14 cells, and the ratio of width to height is 1:5. The rays are narrowest in the California sycamore (pl. XXXVII, *pr*); they average only 5 cells wide, and the ratio of width to height is 1:26. The rays in Arizona sycamore (pl. XXXVI, *pr*) average 8 cells wide, and the ratio of width to height is 1:12. In all species the pith rays abruptly widen in transverse section at the boundary of each annual ring of growth (pl. XXXIII, *pr*). The pith ray cells as seen in radial section are usually much longer than they are high,

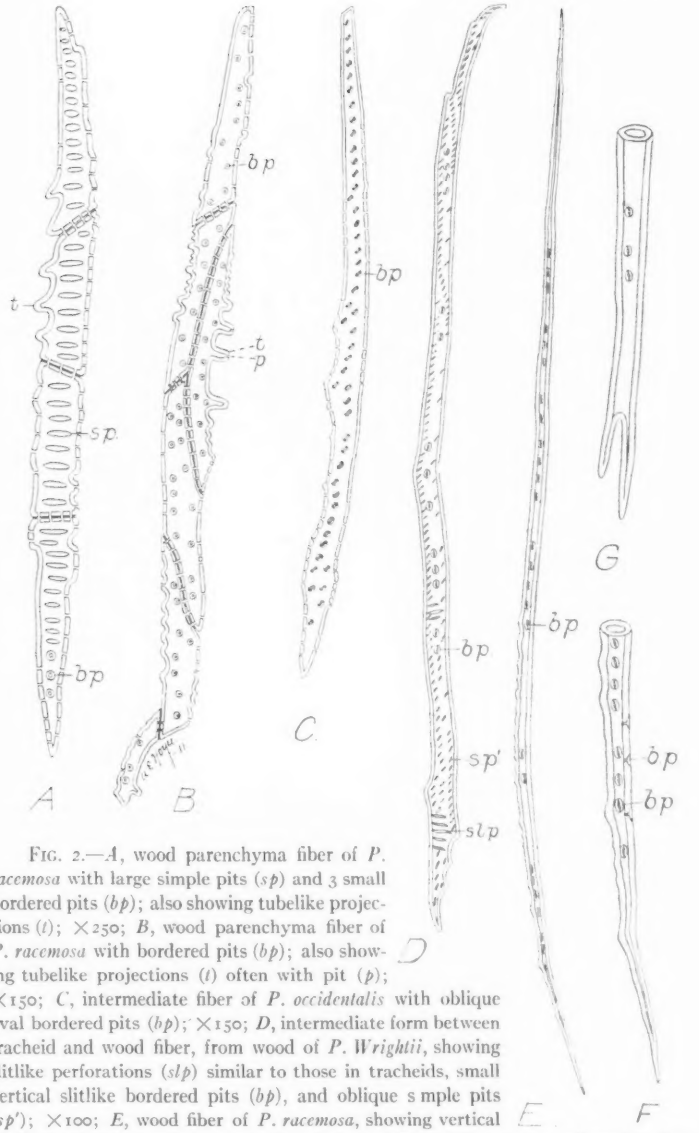

FIG. 2.—*A*, wood parenchyma fiber of *P. racemosa* with large simple pits (*sp*) and 3 small bordered pits (*bp*); also showing tubelike projections (*t*); ×250; *B*, wood parenchyma fiber of *P. racemosa* with bordered pits (*bp*); also showing tubelike projections (*t*) often with pit (*p*); ×150; *C*, intermediate fiber of *P. occidentalis* with oblique oval bordered pits (*bp*); ×150; *D*, intermediate form between tracheid and wood fiber, from wood of *P. Wrightii*, showing slitlike perforations (*slp*) similar to those in tracheids, small vertical slitlike bordered pits (*bp*), and oblique simple pits (*sp'*); ×100; *E*, wood fiber of *P. racemosa*, showing vertical slitlike bordered pits (*bp*); ×100; *F*, end of wood fiber of *P. racemosa* enlarged to show form of bordered pits (*bp*); ×200; *G*, forked end of a wood fiber of *P. racemosa*; ×350.

except toward the outer boundary of each year's growth, where they become very much shorter (pl. XXXVIII, *pr*). The cross-walls between the ray cells are sometimes vertical, but more often they are slightly oblique.

Analytical key

Pith rays 0.22–0.34 mm. wide (average 0.29 mm. or 14 cells); average height, 1.36 mm. or 50 cells; average ratio of width to height, 5.—*P. occidentalis* (pls. XXXII, XXXV, XXXVIII).

Pith rays 0.10–0.22 mm. wide (average 0.16 mm. or 8 cells); average height, 1.84 mm. or 84 cells; average ratio to height, 12.—*P. Wrightii* (pls. XXXIII, XXXVI).

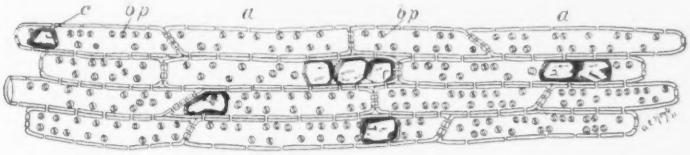

FIG. 3.—Radial view of portion of pith ray of *P. racemosa:* *a*, individual parenchyma cells; *bp*, bordered pits; *c*, crystal; ×200.

Pith rays 0.04–0.20 mm. wide (average 0.09 mm. or 5 cells); average height, 2.36 mm. or 107 cells; average ratio of width to height, 26.—*P. racemosa* (pls. XXXIV, XXXVII).

Individual characteristics

P. occidentalis L., common sycamore
(pls. XXXII, XXXV, XXXVIII)

Distribution.—Southeastern New Hampshire and southern Maine to northern Vermont and Lake Ontario (Don River, near north shores of the lake); west to eastern Nebraska and Kansas, and south to northern Florida, central Alabama and Mississippi, and Texas (Brazos River and thence south to Devils River).

Uses.—Common sycamore is used to a large extent for plug tobacco boxes, furniture, butchers' blocks, ox yokes, wooden bowls, and cooperage, blind wood in cabinet work, chairs, refrigerators,

parquetry, sewing machines, picture molding, saddletrees, vehicles, and bookcases. It is cut radially for veneer. This is because the "silver grain," made by the large pith rays, is very prominent, thus giving the appearance of oak.

Gross characters.—The wood is moderately hard and heavy, not strong, close-grained, very tough, usually exceedingly cross-grained, difficult to split, and not durable in contact with the soil. It is easier to split when dry, but is liable to warp in seasoning. The heartwood is a reddish brown, especially in older trees, with a decidedly reddish color in the pith rays; the sapwood is light brown, and the transition from sapwood to heartwood is quite gradual. The annual rings of growth (pl. XXXII) are less clearly defined than in the two western species. The pith rays are very conspicuous (pl. XXXII, *pr*).

Vessels (transverse section, pl. XXXII, *v*).—These occur either singly or else in irregular groups of 2–5. The last arrangement is the usual one in the early wood. At the beginning of each annual ring and immediately adjacent to the several rows of much radially flattened wood fibers which mark the end of the preceding growth layer is an interrupted row of tangentially compressed vessels (pl. XXXII, *v*) somewhat larger than those formed later. The vessels diminish slightly in diameter and in number toward the outer part of the annual ring, where they are usually isolated. They measure 0.06–0.10 mm., with an average of 0.083 mm. in diameter (table II). Vessel segments (tangential section, pl. XXXV, *v*) vary from 0.72 to 0.89 mm. in length, with an average of 0.786 mm. (table III). The vessel walls are much thinner than those of the surrounding cells. Where two segments join endwise, the opening between them is large and elliptical, or often the end walls are not completely absorbed, leaving a scalariform or ladder-like opening, with 1–25 bars like those found in the ends of the tracheids (fig. 1, *B*). These bars are much narrower than the openings or slits between them and are often branched. The oblique end of the vessel segment is often prolonged, forming a projection which overlaps the adjoining segment above and below. The vessel walls are marked by vertical and horizontal rows of numerous small, slit-like, bordered pits, which are horizontal, or often slightly oblique.

These serve as means of communication between vessels. Large transversely elongated, oval, simple pits connect the vessels with wood parenchyma fibers (fig. 1, *A*, *sp*).

Tracheids (pl. XXXII, *t*).—These are numerous and variable in form, and all gradations between vessels and wood fibers may be found. True tracheids have numerous slightly oblique, elliptical, or slitlike simple pits (fig. 1, *E*, *sp*) throughout their entire length, and at both ends there are many long slitlike openings where they overlap other tracheids above and below (fig. 1, *E*, *slp*). In addition to these pits of the true tracheids most tracheids possess rows of slitlike bordered pits and the transverse oval simple pits found in vessels (fig. 1, *D* and *A*, *sp* and *bp*); hence they somewhat closely resemble vessels. Also many of the tracheids have at one or both ends a simple perforation (fig. 1, *D*, *p*) either with or without bars, like those in vessels, in place of the slitlike openings found in true tracheids, or else the perforation at the end may be intermediate between the slitlike and scalariform types (fig. 1, *D*, *scp*). Tracheids are also found which resemble wood fibers, but these are not numerous. They possess, in addition to the oblique simple pits of tracheids, the small vertical or often slightly oblique slitlike bordered pits which characterize wood fibers (fig. 2, *D* and *E*, *bp*). These tracheids are usually more or less pointed at both ends and sometimes possess small slitlike perforations similar to those found in true tracheids (fig. 2, *D*, *slp*).

Wood fibers.—These are round, angular, or flattened in transverse section (pl. XXXII, *wf*). They are long, slender, and long-acuminate at the ends, and are marked by numerous small slitlike, obscurely bordered pits[4] (fig. 2, *E* and *F*, *bp*). The pits are vertical or oblique, often at an angle of 45°, the oblique position being greatest in fibers with wide lumina. The ends are sharply pointed and often conspicuously forked (fig. 2, *G*). They vary from 1.39 to 2.02 mm. in length, with an average of 1.63 mm. The broad thin-walled wood fibers, as already described, often show a resemblance to tracheids.

Wood parenchyma fibers.—These have acute ends, are moderately thin-walled, and are composed usually of 4–8 individual cells.

[4] The border is hardly visible where the fibers have been isolated by maceration.

Two types of wood parenchyma fibers may be distinguished in the wood of the sycamores, although these may grade somewhat into each other. The elements of one of these types are found adjacent to vessels, which they somewhat resemble and with which they communicate through horizontally elongated elliptical simple pits (fig. 2, *A*, *sp*). Small dotlike or circular bordered pits are also sometimes found in these elements which put the wood parenchyma fibers in communication with one another. The cross-walls between individual cells are usually slightly oblique and are pierced by numerous slightly bordered pits. The second type is larger, usually more tapering at the ends, and the individual cells composing it vary considerably in size and form, so that frequently one individual cell is found overlapping two other cells of the same fiber (fig. 2, *B*). The cross-walls are usually oblique, often approaching the vertical, so that the individual cells are often pointed at the end. This type is characterized by small round or dotlike, slightly bordered[5] pits (fig. 2, *B*, *bp*), which put them in communication with pith ray cells and other wood parenchyma fibers. The walls in certain places are often locally thickened.

Wood parenchyma fibers slightly separated by two contiguous vessels often connect by means of tubular outgrowths from their lateral walls (fig. 2, *A* and *B*, *t*). By means of these tubular projections, which are usually pitted at the points where they join, wood parenchyma fibers communicate with one another. Frequently these projections end blindly.

Intermediate fibers (fig. 2, *C*).—These resemble wood parenchyma fibers in the fact that their walls are irregularly thickened and that their ends are somewhat blunted. They more closely resemble the wood fibers in form, although broader and much shorter

[5] By some investigators a pit is considered bordered only when the pit canal widens out abruptly toward the outside of the cell wall, the outer portion forming an angle with the inner portion of the pit canal which opens into the lumen; where no such widening occurs the pit is simple. On this basis, however, all transitional forms between simple and bordered pits can be found in wood cells; hence the classification is merely an arbitrary one. It is thought best in the present paper to consider pits as bordered where the walls of the pit canals are not parallel and where they give the appearance of a border in longitudinal sections.

than the average wood fiber. They have numerous oval oblique bordered pits.

Pith rays (pls. XXXII, XXXV, XXXVIII, *pr*).—These are very conspicuous. They are on the average 14 cells (0.29 mm.) in width and are about 5 times as high. The pith ray cells are elliptical in the tangential section and are usually much elongated radially. The side walls are thickened and marked by many dotlike slightly bordered pits which place them in communication with the surrounding elements (fig. 3, *bp*). Crystals are very abundant in the pith ray cells.

P. Wrightii S. Wats., Arizona sycamore
(pls. XXXIII, XXXVI)

Distribution.—Southwestern New Mexico and southern Arizona, Mexico (Sonora).

Uses.—The wood of Arizona sycamore is little used. This is on account of its small dimensions and the limited supply of suitable saw logs. It is very similar in its chief structural characters to the wood of California sycamore. While this wood does not occur in the market, it possesses qualities useful for the same purposes as the wood of the common sycamore, and it could be applied to these uses were the tree larger and sufficiently abundant to warrant its exploitation.

Gross characters.—The wood is somewhat lighter and softer and also less cross-grained and easier to split than that of the common sycamore. It is weak, very close-grained, and quite tough, but not very durable in contact with the soil. The sapwood is light colored or almost white, and the heartwood is light brown with a reddish tinge. The annual rings (pl. XXXIII) are clearly defined on a smooth transverse section. The pith rays are clearly visible, though not as prominent as those of the common sycamore.

Minute characters.—Vessels in transverse section (pl. XXXIII, *v*) are arranged singly or in groups, just as in the common sycamore already described. In the beginning of the early wood the vessels

form a fairly continuous row, but they gradually diminish in diameter and in number as they enter the late wood. They vary from 0.04 to 0.09 mm., with an average of 0.076 mm. in diameter (table II). The vessel segments are relatively short in this species, varying from 0.39 to 0.73 mm., with an average of 0.55 mm. in length (table III). Where two vessel segments join end to end the perforation is as in the common sycamore. *Tracheids* (pl. XXXIII, *t*) are variable in form, some closely resembling vessels and others very similar to wood fibers. *Wood fibers* (pl. XXXIII, *wf*) form the bulk of sycamore wood. The length of these elements in Arizona sycamore varies from 1.5 to 2 mm. in length, with an average of 1.7 mm. They are thick-walled and pitted as in the common sycamore. The *wood parenchyma fibers* and *intermediate fibers* of Arizona sycamore are similar in all respects to those of the other two species (fig. 2, *A*, *B*, *C*). *Pith rays* (pls. XXXIII, XXXVI, *pr*) are conspicuous; the average of the large rays is 0.16 mm. wide and about 12 times as high, and therefore much narrower and somewhat higher than in the common sycamore. The pith ray cells are round in the tangential section (pl. XXXVI, *pr*), and are usually much elongated radially.

P. racemosa Nutt., California sycamore
(pls. XXXIV, XXXVII)

Distribution.—California (from the lower Sacramento River through interior valleys and coast ranges) to Lower California (San Pedro Martir Mountain).

Uses.—California sycamore wood, because of its limited supply, is used only locally and only to a small extent. It is somewhat lighter in weight and in color than the common sycamore, and is also less cross-grained and hence easier to work. Users of this wood claim that it is more durable and is also less liable to warp than the common sycamore. It should be useful for all purposes for which common sycamore is used except where great toughness is required, as in butchers' blocks, ox yokes, wooden bowls, etc. It should be found useful especially for tobacco boxes, for which the wood of the eastern sycamore is so extensively used.

Gross characters.—In general appearance the wood is similar to that of Arizona sycamore, although it is slightly lighter, softer, and more durable. Although moderately tough, somewhat cross-grained, and rather difficult to split and work, it is relatively weak. The heartwood is light brown, slightly tinged with red; the sapwood is light yellowish brown. The annual rings of growth are more or less clearly defined on a smooth transverse section (pl. XXXIV). The pith rays (pl. XXXIV, *pr*) appear as numerous conspicuous thin lines.

Minute characters.—Vessels (pl. XXXIV, *v*) are quite evenly distributed throughout the annual rings of growth and are grouped as in the other two species already described. The beginning of each annual ring is marked by a well defined row of slightly tangentially flattened pores larger than those formed later. They measure 0.06–0.09 mm. in diameter and average 0.073 mm. (table II). The average length of vessel segments is 0.677 mm., varying from 0.61 to 0.75 mm. in length (table III). Tracheids (pl. XXXIV, *t*) do not differ from those in the other two species described and show the same transitional forms to vessels and wood fibers. *Wood fibers* (pl. XXXIV, *wf*) are from 1.26 to 1.93 mm. long, with an average length of 1.55 mm. (table IV). *Wood parenchyma fibers* and *intermediate fibers* are in all respects similar to those of the other two species (fig. 2, *A*, *B*, *C*). *Pith rays* (pls. XXXIV, XXXVII, *pr*) are conspicuous in all sections. They are narrowest in this species and have an average width of 5 cells (0.09 mm.). They are on an average 26 times as high as wide, being thus much higher than in the other two species. The pith ray cells in the tangential section are round and slightly higher than broad.

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EXPLANATION OF PLATES XXXII–XXXVIII

PLATE XXXII.—Transverse section of wood of common sycamore (*P. occidentalis*), showing parts of two annual rings of growth; *ew*, early wood; *lw*, late wood; *v*, vessels; *wf*, wood fibers; *pr*, pith rays.

PLATE XXXIII.—Transverse section of wood of Arizona sycamore (*P. Wrightii*), showing parts of two annual rings of growth: *ew*, early wood; *lw*, late wood; *v*, vessels; *wf*, wood fibers; *pr*, pith rays.

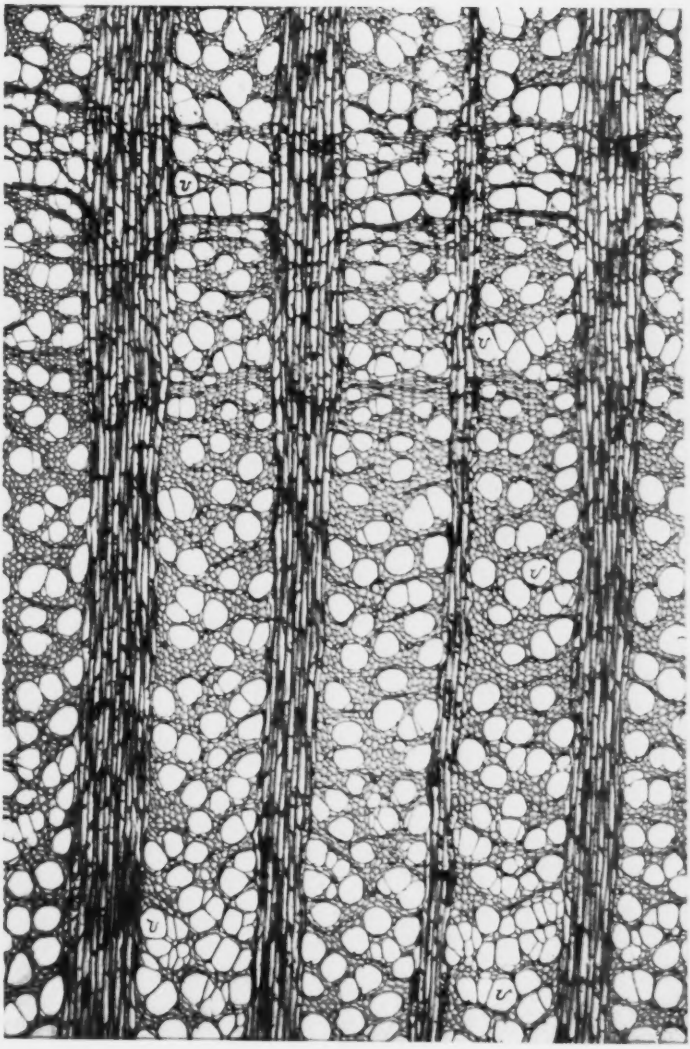
PLATE XXXIV.—Transverse section of wood of California sycamore (*P. racemosa*), showing parts of two annual rings of growth: *ew*, early wood; *lw*, late wood; *v*, vessels; *wf*, wood fibers; *pr*, pith rays.

PLATE XXXV.—Tangential section of wood of common sycamore (*P. occidentalis*), showing pith rays (*pr*) in cross-section and vessels (*v*) and wood fibers (*wf*) in longitudinal section.

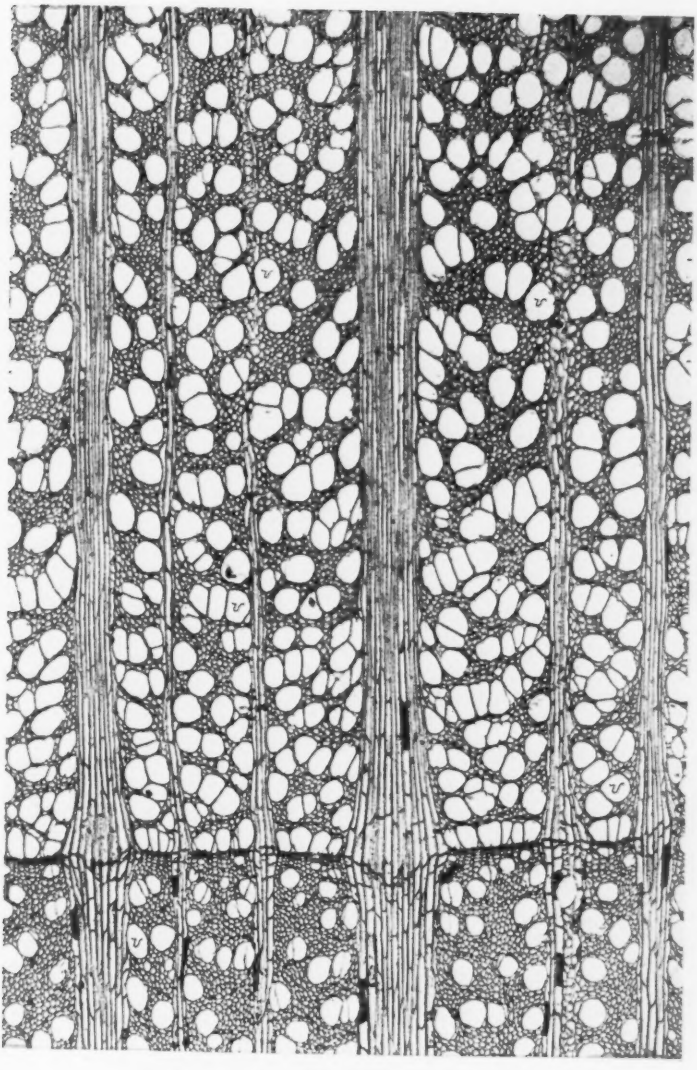
PLATE XXXVI.—Tangential section of wood of Arizona sycamore (*P. Wrightii*): *v*, vessels; *wf*, wood fibers; *pr*, pith rays.

PLATE XXXVII.—Tangential section of wood of California sycamore (*P. racemosa*): *v*, vessels; *wf*, wood fibers; *pr*, pith rays.

PLATE XXXVIII.—Radial section of wood of common sycamore (*P. occidentalis*): *v*, vessels; *wf*, wood fibers; *pr*, pith rays.



BRUSH on SYCAMORE WOODS



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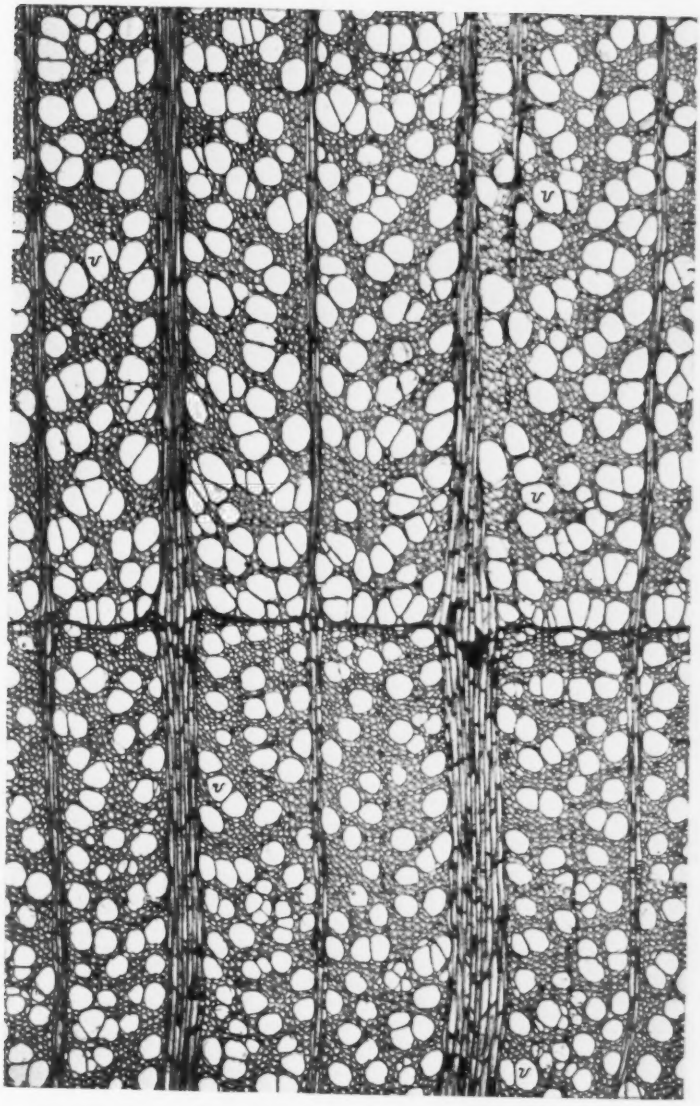
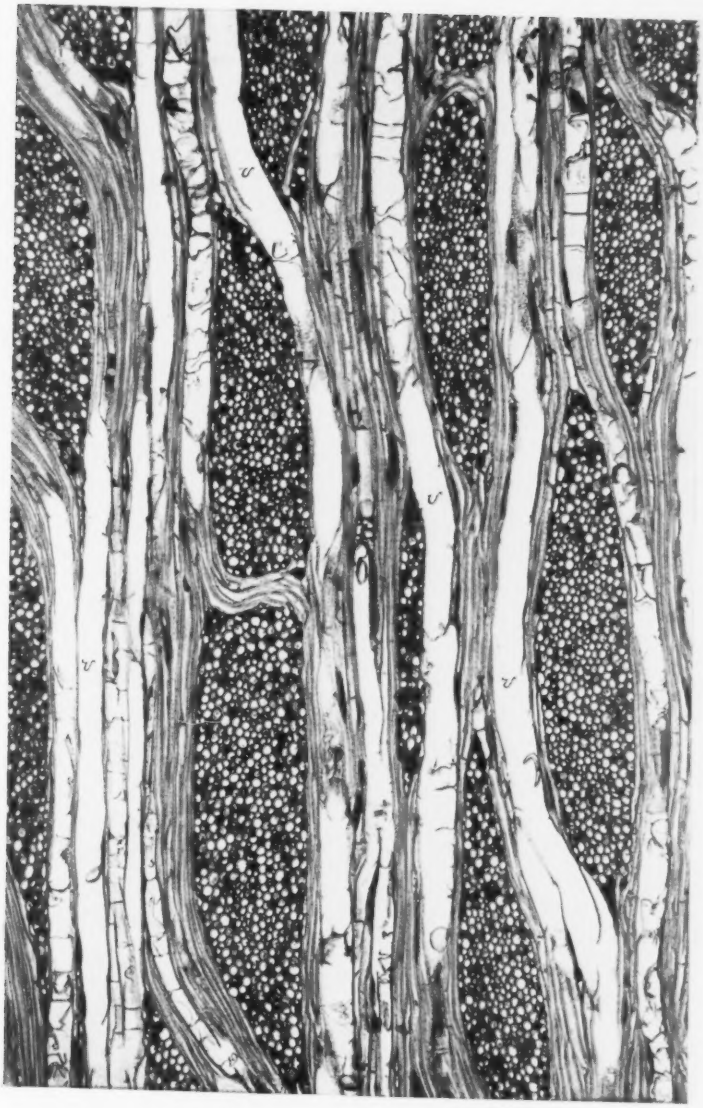


BRUSH on SYCAMORE WOODS



BRUSH on SYCAMORE WOODS

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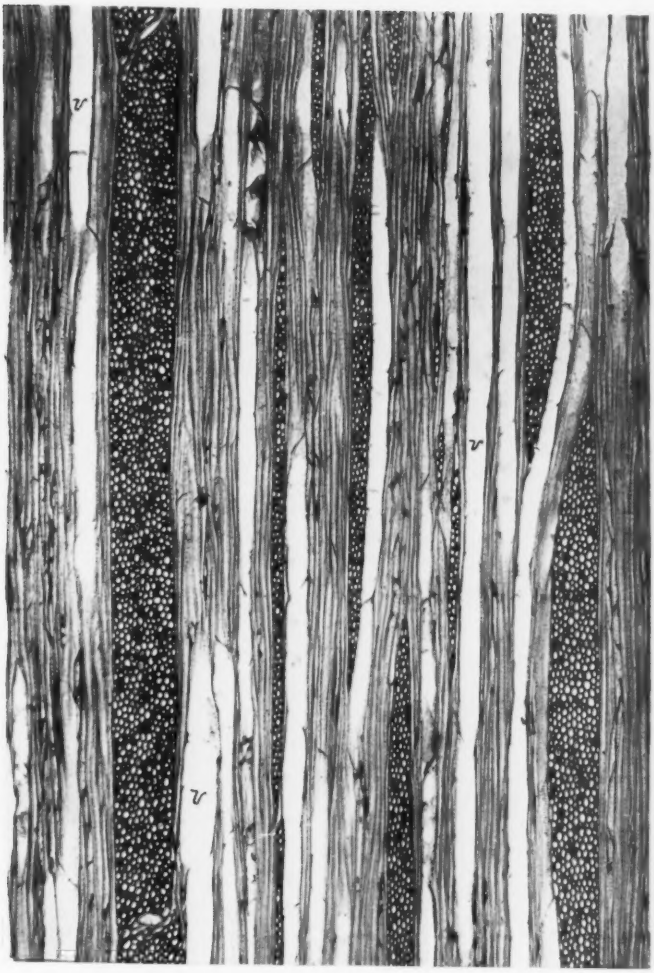
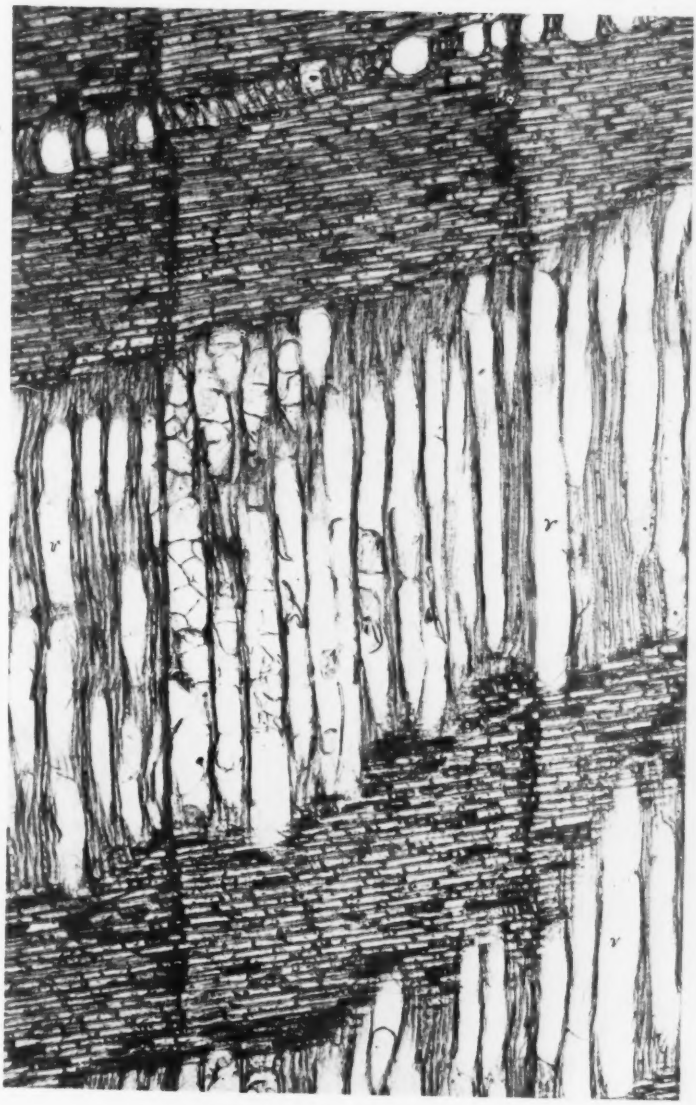


BRUSH on SYCAMORE WOODS



BRUSH on SYCAMORE WOODS

AGENCY OF FIRE IN PROPAGATION OF LONGLEAF PINES

E. F. ANDREWS

(WITH FIVE FIGURES)

The important part played by forest fires in the life history of the longleaf pine has been recognized by a number of recent writers, and HARPER[1] even goes so far as to say "that if it were possible to prevent forest fires absolutely the longleaf pine . . . . would soon become extinct." The connection between the periodic recurrence of these catastrophes and the success of the pine seedlings in competing for possession of the soil was pointed out by Mrs. ELLEN CALL LONG, of Tallahassee, more than 25 years ago, but the suggestion appears on the face of it so at variance with universal experience as to give little occasion for surprise that it should have been received with incredulity, or at best with indifference, by those unacquainted with the adaptive provisions of the species and the conditions prevailing in its habitat.

The writer has recently been favored with exceptional opportunities for investigating this subject by means of an experiment carried out by nature herself, in the native home of the longleafs, with all the exactness of detail that could be expected in a well ordered laboratory. Even that refined test of scientific accuracy, a control experiment, was provided by a neighboring group of the same species that was not exposed to fire on the occasion referred to. The scene of this spontaneous demonstration lies on the northern slope of Lavender Mountain, in Floyd County, Georgia, a ridge of the Southern Appalachians which is certainly very near, if not actually itself, the extreme inland and upland limit of the longleaf pines as they occur at present. The crest of the ridge, according to the United States Geological Survey, attains a maximum height of 1695 ft. above sea level, and extends for 12 miles or more in an approximately east and west direction. It is divided

[1] Economic Botany of Alabama, Part 1, p. 26.

transversely by three deep depressions, or gaps, through which traffic is carried on, and the intervals between the gaps are subdivided by numerous ravines into more or less widely separated spurs and knobs. The southern slopes are covered with the remains of great forests of this valuable timber, interspersed with various hardwood trees and with shortleaf pines (*P. virginiana* and *P. echinata*).

FIG. 1.—Young longleaf pines reforesting mountain side after removal of ripe timber

They have repeatedly been cut for lumber and burned over by "ground fires" started in spring by farmers to provide a free range for their cattle, but the longleafs continue to reproduce themselves with a pertinacity which, if not too diligently thwarted by the blundering incompetence of county officials and the shortsighted greed of ignorant timber cutters, will in the course of a generation or two repopulate the southern mountain slopes with a new forest growth sprung from the old stock (fig. 1).

While there are traditions of the former presence of this species on the northern side of the mountain, the only traces of them that I have been able to find there consist of two small, isolated groups which furnished the apparatus for nature's instructive experiment alluded to. They are situated on opposite sides of a deep ravine which starts near the top of the mountain, at Fouché Gap (the westernmost of the three passes), and descends in a gradually widening rift to the bottom. The larger and more important of these groups occupies a portion of a steep incline between the crest of the ridge and a now abandoned road that winds along the eastern edge of the ravine. It numbered only five individuals, so far as could be seen when I first took note of them, in the summer of 1913. Of these, the rugged patriarch shown in the center of fig. 2, together with two smaller specimens in the background, one of them a mere sapling, were the only members of the colony conspicuous enough to attract the attention of any but a particularly interested observer. The other two were seedlings not over 4–5 dm. in height, and at this stage of development, when the needles are the only part above ground, so like the coarse grasses around them that even an expert, unless keenly on the lookout, would be liable to pass them by unnoticed (fig. 3).

This group of five individuals was scattered over an area of half an acre, more or less, on the edge of an open copsewood which has repeatedly been cut for timber and cleared of undergrowth by minor forest fires. The rest of the declivity, from the gap to the crest of the ridge, had been cleared several years before for cotton planting, but after a short trial was abandoned as too rugged for cultivation. It was at this time (July 1913) neck deep in weeds, mixed with a scrub growth of brush and brambles; and not being in quest of the zoological specimens likely to abound in such places, I did not explore this jungle until two years later, after one of the periodical spring fires had cleared the ground.

The second group, which served as the "control," is situated on the farther side of a low spur or knoll, separated from the neighboring colony by the intervening ravine and the wooded crown of the knoll. It included, when first observed, four individuals, three of which were adults of full cone-bearing age, the

largest one measuring 2 m. in girth. The offspring of these was limited to one solitary seedling, a disproportion the significance of which will be apparent later, when compared with the progeny of the "patriarch" on the other side of the gorge. The soil in both situations is the same, a hard, dry, rocky clay, with a characteristic

FIG. 2.—In foreground, small portion of old clearing as it appeared after fire, with "patriarch" on border between it and copsewood; tall *Pinus echinata* dimly outlined at extreme left stands near brow of opposite slope of ravine; beyond is knoll on farther side of which "control" group is situated.

ground cover of *Pteris aquilina*, *Tephrosia virginica*, and a number of coarse grasses that have a strikingly familiar aspect to one acquainted with the vegetation of the great pine region of the South Atlantic coastal plain. The typical wire grass (*Aristida stricta*) of

the southern forests is here replaced by a correspondingly arid growth of "old field broom" (principally *Andropogon furcatus*, *A. virginicus*, and *A. scoparius*), with a few sedges (*Scleria triglomerata*, *Cyperus retrofractus*, etc.) intermixed. In fact, the only difference in the environment of the two groups is the isolated position of the knoll,

FIG. 3.—Large clump of spearlike leaves near upper lefthand corner is longleaf seedling; others are grasses that have sprung up since fire; skeleton plant on right and white patches in background are hardwood seedlings and bushes killed by fire that left pine seedling unharmed.

the top of which is protected by an encircling turnpike road and by the wooded slopes of two deep ravines, watered by mountain springs and clothed with a heavy growth of broad-leaved trees, conditions which oppose an effective barrier against the spread of fire.

It was not until April 1915 that I made another visit to these straggling longleaf outposts, which had interested me at first merely as landmarks of what seemed to be the *ultima Thule* of their advance in this direction. But a great surprise awaited me. The region around the gap had recently been burned over, and amid the wreckage of skeleton limbs and blackened stubs to which the weedy jungle in the old clearing was now reduced, there appeared a thriving colony of 33 young longleafs, ranging from a few decimeters to a meter or more in height. This new growth was confined mainly to the old clearing, although the "patriarch," whose progeny it presumably is, stands squarely on the border line between the old cotton field and the copsewood, and had no doubt distributed his favors impartially to both. But the absence of trees in the clearing would naturally facilitate the scattering of seeds in that direction, and during the first year or two, before the weeds and brush began to crowd them out, they would germinate freely in the open ground. I had simply overlooked them on my former visit, for the reason that they were hidden in the jungle, where, after making a successful start in life during the palmy days before their little Belgium was overrun by the horde of weedy invaders, they were at last overpowered by numbers and buried out of sight. Deprived of the sunshine so necessary to this sun-loving race, all save the oldest and strongest among them must have perished but for the timely intervention of their powerful ally, the fire, which swept away all rivals and left the young longleafs in undisputed possession of the soil. That such was the case, we have their own direct testimony, for every one of them bore unmistakable marks of fire. Some were so scorched and blackened that any one unacquainted with the habit of the species would unhesitatingly have pronounced them dead. An examination, however, of a number of the worst injured plants showed that in not a single instance had the growing point been killed, or even seriously damaged.

On the other side of the ravine conditions were unchanged except that a new road had been cut around the knoll since my former visit, almost completely encircling it, and one of the adult pines that stood in their way had been felled by the road builders.

The fire had not spread in this direction, and I had some difficulty in finding again, among the coarse grasses which these nurslings so closely resemble, the solitary seedling upon which the future hopes of the colony depend. A careful search among the undergrowth failed to bring to light any further additions to this decadent family, and, as matters now stand, it looks as though the last remnants of the longleaf forest that once clothed the knoll were doomed to early extinction.[2]

It would, of course, be rash to attribute this result solely to the absence of fires. Various other factors may intervene, among which must be reckoned the infrequency of seeding that characterizes this species, a full crop being produced only at intervals of four or five years. If a forest fire should occur during one of these "lean" periods, it would have comparatively little effect, since there would be few seedlings to take advantage of the opportunity offered, while one closely preceding a season of abundance would prepare the way for a proportionate increase in the longleaf population.

Another fact to be considered is that the early growth of the longleaf seedling is very slow. The main energy of the plant during the first year or two is expended in developing the long taproot which enables it to cope successfully with the poverty of its habitat by making the most of the meager resources of the soil, and later provides a safe anchorage for the towering shaft of the adult tree. The young specimen shown in fig. 4, and scarcely distinguishable as yet from a clump of grass, is not less than two years old, and may be more. But while giving due weight to these considerations, I think that after we have studied the effects of fire a little more closely in those cases where its agency is too obvious to be doubted, we cannot deny that it is, and has been in the past, an important factor in the propagation and distribution of the longleaf pines.

In July and August of the same year (1915) I made a longer stay on the mountain, during which time I was able to continue my observations on the pines to better advantage. In the lower

[2] Later observations (September 1917) show a flourishing group of 66 saplings and seedlings in the first colony; while the lower one on the knoll has been reduced to 2 individuals by the loss of the seedling and one of the adult trees.

group, on the knoll, there was little of interest to record, everything remaining very much as when I last saw it. On the upper slope, however, matters were very different, and a more exact count brought the census of the new generation up to 40. Of this number, all of those within the old clearing must have germinated during the 7 or 8 years since the cultivation of this part of the land

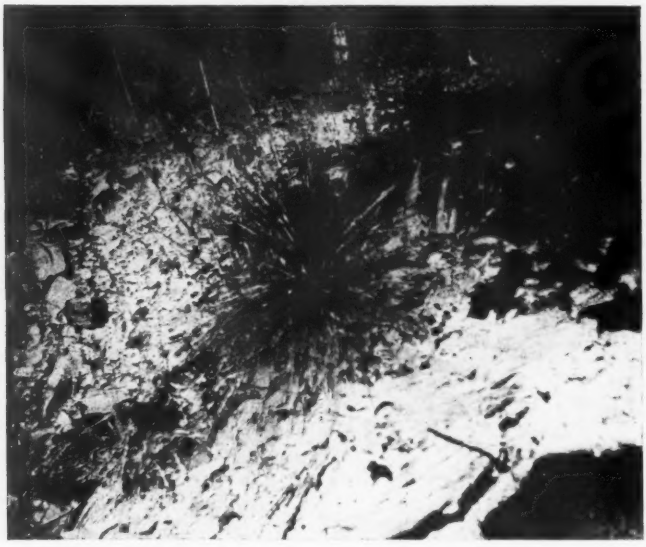


FIG. 4.—Thrifty longleaf seedling that has established itself successfully on stratum of almost solid rock, made possible by long taproot reaching far down into subsoil.

was abandoned, for they would assuredly have been weeded out had any of them dared to show their heads above ground where "cotton was king." To estimate the ages of different individuals with accuracy, however, is not easy, on account of the great irregularity in the rate of growth. While very slow during the first 2 or 3 years, as already pointed out, it becomes proportionately rapid after the critical period of "infant mortality" is past. The growth for the year 1915, up to the first of August, on two saplings of 2.75 and 2 m. in height respectively, was found by measurement

to be approximately 8 and 7.5 dm., while seedlings 12–18 cm. high showed a gain of only 2–4 cm. for the same period.

These figures show that the young longleaf, after attaining adolescence, is fully capable of holding its own in the competitive strife of the plant world. The chief danger to the species in this unceasing contest is in the risk that the seedling, during its long period of infancy, may be starved and crowded to death by the rapidly advancing host of weeds and bushes that outstrip it in the battle for food and sunlight. Their only safeguard against these enemies is, as we have seen, the forest fire.

This naturally brings up the question, how does it happen that the young pines themselves are not killed by the heat which destroys their hardier competitors? The answer is before our eyes. The great rosettes of bristling needles, which give to the longleaf pine its venerable aspect, are not the mere decorative emblems of ancient descent that they seem. They are fulfilling the important function of a defensive armor against the most destructive enemy (after man) that the plant population of the world is exposed to. The young of most species quickly succumb at the first onset of even an ordinary ground fire; but the longleaf pine seedling has its growing point closely enveloped in a crown of spearlike needles, as shown in fig. 4, before the stem begins to rise above the ground. These may be anywhere from 20 to 40 cm. long, including the sheaths, which average about 3–4 cm. When fresh they ignite so slowly as to be practically incombustible. Strictly speaking, they can hardly be said to ignite at all, but are bitten off and consumed where the fire comes in contact with them. Moreover, the application of heat causes a violent sizzling and contortion of the parts affected, accompanied by a series of small explosions which are sometimes capable of extinguishing a match; and I have even known them, on one occasion, to put out the flame of a candle. At another time, I was trying to ignite a fresh "pinetop" (as these tufts are called in our Georgia vernacular) by the flame of a kerosene lamp, when it fumed and sputtered and caused such a commotion in the burning wick that I cut short the experiment for fear of exploding the lamp and transferred my operations to the kitchen. There was a slow wood fire in the

stove, into which I thrust the pinetop, and awaited results, watch in hand. When I removed the stub at the end of 4 minutes, the needles had all been consumed, but the sheaths, especially those of the vigorous young fascicles crowded around the growing point, remained for the most part intact. The bud itself, though considerably scorched and blackened externally, appeared, like the stem, not to have suffered beyond the possibility of recovery, though this point, as the final result will show, was open to doubt.

It may be explained here that in excursions through the mountains it is desirable to avoid all unnecessary encumbrances in the way of luggage, and, as the conditions of life are very primitive in the regions of greatest interest to the botanist, one often has to resort to homely makeshifts when supplementing observation by experiment. It is surprising, however, what interesting results may sometimes be obtained by very simple means when one is determined to get to the bottom of a thing.

To complete the experiment, I next placed a couple of fresh pinetops in an upright position over a brisk blaze of chips and twigs out of doors, so as to approximate, as closely as possible, the normal conditions of an ordinary brush fire. After 8.5 minutes, when the flame had subsided and the needles were all burned away, down to their sheathed bases, I placed the stubs in water, together with the one that had been subjected to the ordeal of the kitchen stove on the day before. At the end of 12 days, when my stay on the mountain came to an end, the latter was found to have sustained internal injuries which left it in all probability beyond recovery. The other two came out of the fiery ordeal, if not altogether unscathed, yet with an appearance of vitality sufficiently unimpaired to warrant the presumption that had they remained attached to the living stem, like their kindred in nature's outdoor experiment, they would, like them, quickly recover from the effects of the fire.

The effectiveness of this provision for the safety of posterity is further assured by the tendency of the needles to persist on the stem of the young shoot for several years, until the more delicate parts are lifted beyond the reach of danger. As the growth of the sapling progresses, and the increasing thickness of the bark provides for the protection of the stem, the needles become massed

around the growing axes at the end of the branches, where they form the tassel-like clusters or "pinetops" which are such a striking characteristic of the longleaf pines (fig. 5). Under the influence of light the lateral stems supporting these tassels tend to curve upward. This upright position has the advantage that the fire, which

FIG. 5.—Young longleaf pine with stem surrounded by bristling *chevaux-de-frise* of needles, growth of several successive years.

ordinarily makes its attack from below, has to cut its way through the entire phalanx of protecting needles before it can reach the growing point. If the rosettes were drooping as in the winter condition of the white pine, they would, instead of protecting the buds, act as refractors to converge the heat upon them.

With such efficient fire protection it can easily be seen why the longleaf seedling is able to withstand a degree of heat that would be fatal to older and in other respects hardier plants. The same facts also explain why, in a state of nature, these trees tend either to congregate in pure forests over large areas or to become extinct if exposed to unrestricted competition with hardwoods. In the latter case the older conifers may hold their own for a time, but as these die out from superannuation or other causes, the new generation that should replace them, unable to develop in the shade, and cut off from the sunlight by the broad leaves of the hardwoods, fails to reach maturity and the race in time becomes extinct. On the other hand, when forest fires, especially of the minor type known as "ground fires" and "brush fires," occur at not too frequent intervals, the immunity of the pines enables them to take the lead in the work of reforestation, and through the gradual elimination of their rivals to become finally the sole possessors of the soil.

ROME, GA.

PERMEABILITY OF THE CELL WALLS OF ALLIUM

S. C. Brooks

Many investigators have reported that the tissues of higher plants are almost if not quite impermeable to inorganic salts. They have usually attributed this phenomenon to the impermeability of the protoplasm to the salts used. It is quite probable, however, that the cell walls themselves may exert an important influence on the permeability of tissues. It is of interest, therefore, to point out a striking example of the impermeability of the cell wall, which was found when it was attempted to investigate, by the diffusion method recently described by the writer,[1] the permeability of epidermis from the inner surface of bulb scales of the onion. The principle of the experiment and the apparatus used were the same as in the writer's experiments on *Laminaria*, as recorded in the paper cited. Certain modifications were necessary, however.

In order to avoid injury due to drying out of the epidermis (which consists of a single layer of cells), it was necessary to reduce as much as possible the time intervening between the act of stripping the epidermis from the scale and that of filling the cells with solutions. The whole operation usually occupied about 30 seconds, a time which caused no observable injury to the cells.

Dead material was prepared by exposing freshly removed sheets of tissue to chloroform vapor for a period of one hour, then immediately immersing them in a large volume of distilled water, which was several times renewed. After 15 days in distilled water the dead tissue was used in the usual manner.

The salt solutions used in the lower cells were always 0.05 M, a concentration hypotonic to the living cells of the onion epidermis. In the upper cells there was placed distilled water having a specific conductivity of about 2×10^{-6} mhos. Extreme precautions were used to prevent access of dust, acid vapors, or any other soluble material to the distilled water in the upper cells. In all the

[1] Brooks, S. C., A new method of studying permeability. Bot. Gaz. **64**: 306–317. *figs. 2.* 1917.

experiments on this tissue the distilled water was obtained by distillation from an apparatus made entirely of glass, and which had been in constant operation for several weeks prior to the collection of the sample here used.[2] All the kations were used in the form of chlorides, thus making it possible to determine their concentration in the upper cell by two entirely independent methods. The conductance of known concentrations from 10^{-7} M to 10^{-3} M of the salts used was determined and a curve plotted showing for each salt the concentrations corresponding to any given conductance. The concentration of a given salt diffusing into the distilled water in the upper cell was then ascertained by comparison of the conductance of the solution in the upper cell with the curve for the corresponding salt. In addition, the chlorides in the upper cell were determined nephelometrically by the method of RICHARDS and WELLS.[3]

In neither living nor dead tissues could the presence of chlorides in the upper cell in excess of 3×10^{-5} M be detected nephelometrically, even during experiments whose duration exceeded 24 hours. The changes in conductivity were also such as would indicate a negligible increase in the concentration. It seems therefore that little or no salt can pass through the epidermis.

Experiments were then tried to determine the permeability of the tissue to dyes. The diffusion of Bordeaux red through the diaphragm from an 0.1 per cent aqueous solution in the lower cell into distilled water in the upper during 96 hours was insufficient to cause any visible change in the color of the distilled water. A similar experiment, in which the lower cell contained a 1 per cent aqueous solution of eosin (Merck's eosin bluish), was continued for 7 days; at the end of that time the distilled water in the upper cell could not be distinguished in color from fresh distilled water, even by the use of a colorimeter.

The experiments on dyes (as well as those on acids and alkalies, subsequently described) were performed on dead tissue.

[2] Water distilled from glass becomes better the longer distillation is continued, since the constant exposure to steam and hot water soon removes the more soluble constituents of the glass. Water such as that here used may be regarded as having no appreciable toxicity.

[3] RICHARDS, T. W., and WELLS, R. C., The nephelometer, an instrument for detecting and measuring opalescent precipitates. Amer. Chem. Jour. **31**:235. 1904.

In the use of indicators we possess an extremely sensitive and reliable means of demonstrating the presence of small amounts of free acid or alkali in a solution. It would be possible therefore to detect the diffusion through the diaphragm of tissue of small amounts of hydrochloric acid or sodium hydroxide by adding a small amount of a suitable indicator to the distilled water in the upper cell of the apparatus. In the lower cells 0.1 M solutions of the acid and alkali were used.

A period of 43 hours was insufficient to allow the passage of an amount of sodium hydroxide great enough to cause any change in the color of the distilled water containing about 0.01 per cent of phenolphthalein, as determined by comparison in a colorimeter with fresh distilled water. The change of hydroxyl-ion concentration necessary to cause the first visible change in the color of the phenolphthalein would be that from 1×10^{-9} M to 1×10^{-5} M.

The turning point of Congo red lies at a hydrogen-ion concentration of 1×10^{-4} M. An increase of less than 1×10^{-4} M in the hydrogen-ion concentration of distilled water containing Congo red will then cause the appearance of the blue coloration in the indicator. Experiments were conducted in which the lower cells were filled with 0.1 M hydrochloric acid, and the upper cells with distilled water containing barely sufficient Congo red to cause a distinct red coloration; these showed that a period of 3–5 hours was sufficient to cause the color change in the indicator. Control experiments in which the lower cell was filled with pure distilled water showed no color change in the upper cells during 19 hours.

In order to eliminate the possibility that the permeability to hydrogen ions was the result of the action of the 0.1 M hydrochloric acid on the tissue, several of the cells in which there had been a diffusion of acid were simply rinsed out thoroughly, and the lower cell finally filled (after preliminary rinsing with the solution) with 0.1 M sodium hydroxide. The upper cell was filled with distilled water containing a slight amount of phenolphthalein. There was no color change in the distilled water up to the end of the experiment, a period of 3 days.

The inner epidermis of onion bulb scales, at least when its cells are dead, is therefore but slightly permeable to hydrochloric acid, and not perceptibly so to any other of the substances tried. These

included sodium, calcium, and aluminium chlorides, Bordeaux red, eosin, and sodium hydroxide.

This extraordinary impermeability is confined to the exterior cell walls of the epidermis, as will be seen by the following simple experiment. A sheet of epidermis stripped from the scale and mounted in water on an ordinary microscope slide, then irrigated with a 0.4 M sodium chloride solution, was strongly plasmolyzed within 30 seconds. In order that plasmolysis should occur, it was necessary that the plasmolyzing solute should pass into the space between the cell wall and the retracted protoplast. Some part of the cell wall is therefore freely permeable to sodium chloride.

Pieces of the scale, about 2 cm. square, with the epidermis still in place, were then placed in a 0.4 M sodium chloride solution. At intervals up to 30 minutes pieces were withdrawn, the surface dried with filter paper, and a small piece of epidermis from near the center of the piece of scale removed. These were placed between a microscope slide and cover slip, no water being added, and in all cases their cells were found to be wholly normal in appearance; but a few seconds' irrigation with an 0.4 M. sodium chloride solution now sufficed to cause violent plasmolysis. These experiments show that the exterior walls of the epidermal cells form a continuous layer highly impermeable to most substances and comparable to certain seed coats as described by previous investigators.[4]

Summary

1. The exterior cell wall of the epidermis from the inner surface of onion bulb scales is slightly permeable to hydrochloric acid, while it is practically impermeable to various salts, dyes, and to sodium hydroxide.

2. It is necessary to consider the influence of impermeable cell walls in interpreting experiments on the permeability of plant tissues.

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HARVARD UNIVERSITY

[4] Cf. BROWN, A., The selective permeability of the coverings of the seeds of *Hordeum vulgare*. Proc. Roy. Soc. London, B **81**:82. 1909; SCHROEDER, H., Über die selektive permeable Hülle des Weizenkornes. Flora **102**:186. 1911; SHULL, C. A., Semipermeability of seed coats. BOT. GAZ. **56**:169–199. 1913.

BRIEFER ARTICLES

PYRENOTHRIX NIGRA, GEN. ET SP. NOV.

(WITH FOUR FIGURES)

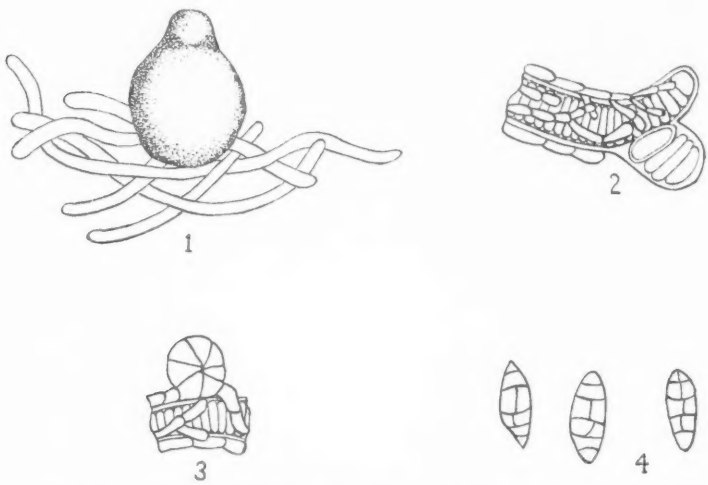
The material upon which the new genus and species of lichens here described is based was collected by Professor ROLAND THAXTER, of Harvard University, in Florida in 1897. I wish to acknowledge my indebtedness to Professor THAXTER for his kindness in placing the material at my disposal for study and description. On account of the distinctive combination of a byssine thallus and a pyrenomycetous fruit this new genus may appropriately be named as follows:

Pyrenothrix, gen. nov.—Thallus crustaceo-byssinus ecorticatus substrato arcte adnatus gelatinosus, ex hyphis tenuibus leptodermaticis crebre septatis ramosis, filamenta gonidiorum dense obducentibus. Gonidia ad species *Scytonemae* pertinentia filamentis implexis. Perithecia tenues coriacea pseudoparenchymatica, integra simplices recta nuda nigrescentia, in gonidiis sessilia nunquam immersa, ostiolis parum distinctis. Paraphyses persistentes simplices filiformes. Asci clavati. Sporae fuligineo-nigricantes murali-divisae cellulis subcubicis. Spermagonia non visa.

This new genus, by reason of having gonidia of the *Scytonema* type and fruit of the perithecial form (figs. 1, 2), would appear to belong most naturally to the family Pyrenidiaceae, as constituted by ZAHLBRUCKNER (ENGLER and PRANTL, Die Natürlichen Pflanzenfamilien, Teil I, Abt. 1, p. 76), but differs from all of the genera of that family hitherto described in the byssine character of the thallus (fig. 1), and in the muriform spores (fig. 4). When examined under the microscope, the structure of the thallus and the relation of hyphae and gonidia are seen to be exactly that of *Coenogonium* (fig. 2). Without entering into the much debated question, "What is a lichen?" it may be said that if *Coenogonium* is a lichen then *Pyrenothrix* is a lichen, as the two are strictly analogous. That the perithecia are not those of a secondary parasite or merely accidentally associated with the filaments of the alga is proved by the observation of early stages in their development showing their origin from the web of hyphae that envelop the gonidia (fig. 3).

Pyrenothrix nigra, sp. nov.—Thallus fusco-nigricans byssinus substrato arcte adnatus late effusus non limitatus, sicco nec flaccido nec

spongioso, madefacto molle gelatinoso, ex hyphis tenuibus (3–4 μ crassis) septatis torulosis crebre ramosis, filamenta gonidiorum crebre obducentibus; gonidiis Scytonematicis filamentis, crassitudine 13–18 μ, vaginis tenuis homogeneis non lamellosis, flexuosis implexis, rarius pseudoramosis. Perithecia minuta, altit. 200–225 μ, crassit. 160–175 μ, pyriformes collo crasso breveque, primum fuliginea demum nigrescentia, ostiolo minute parum distincto. Paraphyses persistentes simplices filiformes sat flexuosae. Asci clavatae, 8-spori. Sporae fumoso-nigricantes,



FIGS. 1–4.—Fig 1, habit sketch, ×41; Fig. 2, end of gonidial filament, showing false branch and some of enveloping hyphae (part omitted for clearness), ×385; fig. 3, early stage in formation of perithecium, ×385; fig. 4, spores, ×385.

oblongae vel late fusiformes, muriformes pauciloculares, 5–6 loculares, 2 locellati, 17–20×6–9 μ.

Thallus brownish-black, spreading over the substratum without definite limits and closely adnate, byssine, when wet soft and gelatinous, when dry harsh and not at all spongy; made up of gonidia of the *Scytonema* type, with flexuose, intertangled filaments, 13–18 μ thick, with a thin, homogeneous sheath and infrequent false branches; the filaments densely covered with septate, torulose, branched hyphae, 3–4 μ in thickness. Perithecia minute, 200–225 μ high and 160–175 μ thick, pyriform with a short, thick neck, and minute, indistinct ostiole; the wall

thin, coriaceous, pseudoparenchymatous, at first fuliginous-brown, then blackening. Paraphyses persistent, simple, filiform. Asci clavate, 8-spored. Spores smoky-black, oblong or broadly fusiform, muriform, 5–6 locular, with some of the cells once divided, 17–20×6–9 μ.

Abundant on the bark of scrub oaks at West Palm Beach, Florida, December 1897 (type!); and on living Oleander at Cocoanut Grove, Florida, November 1897; collected by Professor ROLAND THAXTER. Type specimen in the Cryptogamic Herbarium of Harvard University.—LINCOLN W. RIDDLE, *Wellesley College, Wellesley, Mass.*

CURRENT LITERATURE

MINOR NOTICES

North American flora.—The third part of Vol. 10 continues the presentation of the Agaricaceae by MURRILL,[1] the 12 genera of Pholiotanae being presented, excepting the genus *Inocybe*. The 11 genera presented include 324 species, of which 76 are described as new. The largest genera are *Gymnopilus* (85 spp.), *Naucoria* (65 spp.), *Hebeloma* (50 spp.), *Crepidotus* (46 spp.), and *Galerula* (33 spp.). The remaining 45 species are distributed among 6 genera. New species are described in *Crepidotus* (7), *Tubaria* (4), *Galerula* (8), *Naucoria* (21), *Pluteolus* (4), *Mycena* (2), *Gymnopilus* (13), and *Hebeloma* (17).—J. M. C.

NOTES FOR STUDENTS

Carbon assimilation.—JORGENSEN and STILES[2] have summarized our knowledge of the processes involved in the assimilation of carbon by green plants and the pigments concerned in them. The portion dealing with the pigments themselves has been reviewed by LINK.[3] In the introduction the reviewers express the hope that "the following pages will be of interest to those concerned in the development of scientific agriculture as well as to those interested in plant physiology for its own sake." The discussion of the path of gaseous exchange between the leaf and the surrounding atmosphere is based mainly on the work of BLACKMAN and BROWN and ESCOMBE. The conclusion reached is that the proof is now definite that the stomata are the main path of the intake of carbon dioxide into the assimilating aerial leaf of the higher plants. Any intake that may occur through the cuticle is of very minor importance. Carbon assimilation is regarded as a complex of processes which probably obey quite different laws. Attention is called to the 5 obvious factors upon which the rate of carbon assimilation in the leaf may depend: (1) carbon dioxide supply, (2) intensity of illumination, (3) temperature, (4) water supply, (5) quantity of chlorophyll. To these is added BLACKMAN's time factor. It is found that below 25° C. the rate of carbon assimilation a little more than doubles for each rise of 10° C. For cherry laurel this gives a van't Hoff curve

[1] MURRILL, W. A., North American flora **10**:part 3, pp. 145–226. Agaricales: Agaricaceae (pars), Agariceae (pars). New York Botanical Garden. 1917.

[2] JORGENSEN, I., and STILES, W., Carbon assimilation. A review of recent work on the pigments of the green leaf and the processes connected with them. New Phytol. reprint no. 10. London. Wesley & Son. 1917.

[3] BOT. GAZ. **62**:417–421. 1916.

in which the temperature coefficient for a rise of 10° C. is 2.1. In *Helianthus tuberosus* it was 2.5. Below 25° C. the initial rate is maintained, but above that temperature it falls off regularly. The higher the temperature the more rapid is the falling off. The falling off at any given temperature is most rapid at first and subsequently becomes less rapid.

Since it is thus impossible to measure the highest possible assimilation at high temperatures, BLACKMAN estimates it by plotting his experimental results below 25° C. (a van't Hoff curve in which $Q_{10}=2.1$) and continuing the curve by assuming that the same rule is followed above that temperature. That this curve represents the initial rate above 25° C. is confirmed in BLACKMAN's opinion by plotting on this same diagram (the abscissae now having a time significance instead of a temperature significance) the values obtained for the assimilation rate at higher temperatures, and continuing these curves back to a point representing zero time. It is thus found that the position representing zero time for each curve is also that representing the temperature at which the readings were taken.

On this basis BLACKMAN concludes that there seems to be reason for the preliminary acceptance of the theory that the initial values of assimilation above 25° C. follow the van't Hoff curve as they do below that temperature. JORGENSEN and STILES seem disposed to defend BLACKMAN against all criticisms on this point. It must be remembered, however, that COHEN-STUART[4] has shown that, according to the van't Hoff law itself, values of Q_{10} are not constants and that the velocity is not an exponential function of the temperature. KUIJPER[5] found that such a method as BLACKMAN used on carbon assimilation did not apply to respiration. LEITSCH[6] has also found that it does not apply to temperature and rate of growth.

In regard to the light factor, the conclusion is reached that "where temperature and carbon dioxide supply are in excess the rate of assimilation is in direct proportion to the intensity of illumination." In the case of cherry laurel during the middle of an August day (temperature 20°.5 C.) the maximum assimilation was possible with 36 per cent of full sunlight, while in the case of *Helianthus* 69 per cent was necessary.

Assimilation is shown to increase directly with carbon dioxide supply until some other factor becomes the limiting one. When this point is reached, assimilation remains constant with further increases in carbon dioxide up to 0.0536 per cent. Above this point the rate of assimilation falls off rapidly. BLACKMAN's interpretation is that this is due to the narcotic effect of the strong CO_2 on the protoplasm. The reviewers state that "BLACKMAN carefully avoids premature conclusions and tries to find non-committal expressions which will embody all his experimental results."

[4] Konn. Akad. Wetans. Amsterdam. Proc. Sec. Sci. **14**:1159–1172. 1912.

[5] Rev. BOT. GAZ. **50**:233–234. 1910.

[6] Ann. Botany **30**:25–46.

In discussing WILLSTÄTTER's work on the relation between chlorophyll content and assimilation rate, the reviewers state that "WILLSTÄTTER advances a simple definite hypothesis and attempts to obtain experimental data which will support his theory." WILLSTÄTTER postulates that carbon assimilation consists of two definite processes, one photochemical, taking place in the chloroplast, and one enzymatic, taking place at the boundary between the chloroplast and the plasma. The oxygen is supposedly evolved during the latter process. The experimental proof of this postulate is incomplete. The view is not a surprising one, however, since the relation of carbon assimilation and of enzymatic action to temperature both seem to be special cases of TAMMAN's principle. The surprising thing would be that there should be only two processes concerned. The reviewers state that under certain circumstances, when no other factor is limiting, the amount of chlorophyll determines the intake of CO_2 by the leaf. WILLSTÄTTER found that the amount of pigment is not altered during the process of carbon assimilation.

The discussion of the present status of our knowledge of the known products of assimilation (oxygen and carbohydrates) is based on the work done within the last 31 years, since the earlier workers did not separate the gaseous exchanges due to assimilation from those due to respiration. It seems probable that the real assimilation coefficient (taking respiration into account) approximates unity. In considering the nature of a reaction or a series of reactions, it is very important to know the quantitative relation between initial substances and the final products of the reaction. In carbon assimilation by green leaves the relation between CO_2 taken in and O_2 evolved has not been definitely established.

The reviewers summarize in a table (p. 106) the evidence in regard to the presence of various carbohydrates in the leaf. (1) *Polysaccharides* (exclusive of cellulose and pectic substances); the presence of starch has of course long been well known, and the presence of pentosans and dextrin seems to be established. (2) *Disaccharides;* sucrose is certain, and maltose is doubtful. (3) *Hexoses;* the presence of d-glucose and d-fructose is well recognized. (4) *Pentoses;* none are positively known to be present, although there is some evidence pointing to the presence of l-arabinose and l-xylose. Definite evidence as to what sugars are absent and more quantitative data in regard to the ones present are much to be desired. The reviewers state that there is strong evidence that sugars are the first definitely known products of the assimilatory process, starch probably being a secondary product. Although most workers regard cane sugar as first, there is no satisfactory evidence that the hexoses may not be first. The mechanism of translocation is complex, depending upon differences of enzyme concentration, and possibly upon permeability changes, the nature and causes of which are at present largely unknown. The available data on energy relations are dealt with under three heads: (1) quantitative determinations of materials produced and their heats of combustion, (2) measurement of both radiant energy and heats of combustion, (3) assimilation

power of light of different wave lengths. Under (1) two methods of estimating the products of carbon are discussed: (*a*) increase in dry weight, and (*b*) amount of CO_2 taken in. The reviewers conclude that if the dry weight method can be made more accurate, it should not be lightly abandoned. If we assume with BROWN and ESCOMBE that the heat of combustion of all products of assimilation is the same as that of glucose (3.76×10^3 gram calories), we shall fall into a considerable error, as is indicated by the following values for other substances present in leaves: sucrose 3.99×10^3, starch 4.1×10^3, cellulose 4.2×10^3. If oils are present, the error in this assumption would be still greater. Actual determinations of heat of combustion made by other workers on the products of assimilation in the leaves of various plants give values varying from 4.4×10^3 to 5.2×10^3 gram calories.

Quantitative measurements of radiant energy in relation to the leaf are based on the assumption that the total radiant energy falling upon the leaf is disposed of in the following ways: (1) reflection from the leaf surface, (2) carbon assimilation, (3) transpiration, (4) transmission through the leaf, (5) thermal emission.

BROWN and ESCOMBE (1905) disregard (1) in their calculations. The reviewers believe that this is not negligible, since even a black cloth may reflect 1 per cent of the radiant energy incident upon it. PURIEWITSCH (1914) has estimated (2) in a few cases by measurement of the increased heat of combustion of the leaf per unit area. His highest value was 2.6 and his lowest 1.3 per cent. On the basis of these he calculated other cases, getting as high as 7.7 per cent. BROWN and ESCOMBE calculated (2) by assuming that one gram of absorbed CO_2 is equivalent to 0.64 gram of dry matter formed, and that the heat of combustion of the products of assimilation is 3.76×10^3 gram calories. The accuracy of these assumptions is not confirmed by measurements. Their computed values vary from 0.42 to 1.66 per cent. All of the evidence at hand thus indicates that only a very small percentage of the radiant energy received by the leaf is actually used in carbon assimilation. It might be expected that the proportion of the sun's energy used in assimilation would vary inversely as the intensity of the illumination. This expectation is not justified by the experimental data, and it is clear that we must look for some other factor on which no data are given. The reviewers point out here a case of lack of correlation of effort by investigators. If PURIEWITSCH had taken cognizance of BLACKMAN'S researches, his experiments (although regarded by PURIEWITSCH himself as preliminary) might have yielded results of much greater significance. The energy used in (3) was arrived at by BROWN and ESCOMBE by determining by weight the amount of transpiration and calculating the energy used from the heat of the vaporization of water at that particular temperature. Their results vary from 9.67 to 53.6 per cent. BROWN and ESCOMBE measured (4) directly. Their values quoted by the reviewers vary but little, the highest being 35.32 and the lowest 35.28 per cent. It is evident that (5) will usually have a positive value, since the

temperature of the leaf is usually higher than that of the air. If, however, the temperature of the leaf falls lower than that of the air, the leaf will gain energy from the air, that is, thermal emission will be negative. BROWN and ESCOMBE's values for thermal emission are based on the same set of experiments as the data quoted under (2), (3), and (4). They are all positive. The smallest one is 6.0 and the largest is 54.60 per cent. BROWN and ESCOMBE were the first to attempt to obtain a complete balance sheet for the leaf in regard to energy. Further quantitative data correlating the work of BLACKMAN, BROWN and ESCOMBE, and PURIEWITSCH are greatly to be desired. We still have no reliable data on which any conclusion can be based as to the relative efficiency of the rays in the different portions of the spectrum.

The reviewers mention the early work, indicating that the maximum assimilation takes place in the red part of the spectrum and that there is a secondary maximum in the blue-violet end as being now of only historical interest, since the methods of measuring energy were unsatisfactory and the measurements of assimilation were crude.

The work of KNIEP and MINDER (1909), indicating that blue and red light of the same intensity produce the same assimilation and that the green light is incapable of producing assimilation, is rejected because they give no data relating to any factors other than light intensity, hence some other factor may have been a limiting one. They also reject TIMIARIZEFF'S (1903) data on the absorption of energy by chlorophyll, since he worked with alcoholic extracts, which must have contained less chlorophyll than impurities. The work of BROWN and ESCOMBE on the absorption of radiant energy by the white and the green portion of a leaf of *Negundo aceroides* is also rejected, since it is considered unfair to assume that the conditions in the green and the albino parts are the same except for the presence of chlorophyll. WEIGERT'S (1911) conclusions on the efficiency of the assimilation system are considered unreliable, since they are based on the work of BROWN and ESCOMBE just mentioned.

The reviewers introduce their discussion of theories of carbon assimilation with a sweeping condemnation of theories, making the point that those who have contributed the most valuable data on this subject have not suggested any theories. They cite DE SAUSSURE, SACHS, PFEFFER, and BLACKMAN as examples. They might possibly have added SPOEHR to the list, but they could not have added WILLSTÄTTER, since his data on the pigments of the green leaf are certainly very valuable, and considerable space is given in their review to the discussion of his theories.

Of course blind following of a theory does not lead to progress, and the desirable attitude is that of seeking for facts regardless of their bearing on any theory, but to assume that none of the workers (except SPOEHR) have been influenced by dissatisfaction with the theories that have been advanced seems unwarranted. It is not the right use of scientific imagination that is to be condemned, but the acceptance of mere imaginings as facts. JORGENSEN and STILES, of course, are quite right in their condemnation of whatever

tendency there may have been in textbooks to present BAYER's hypothesis as representing facts.

They discuss the theories and suggestions of four men: (1) the well known theory of BAYER involving formaldehyde as an intermediate product; (2) the suggestion of VAN'T HOFF that assimilation consists of two parts, a photochemical reaction and an enzyme reaction; (3) SIEGFRIED's suggestion that carbon dioxide may form carbamino groups with the protoplasm of the plant cell and that the photochemical reaction may then occur in a complex carbon compound; and (4) WILLSTÄTTER's theories which, so far as they are new, are regarded by the reviewers as rather wild, the most reasonable one suggested by him being merely a repetition of SIEGFRIED's suggestion.

In the end it appears that we have at present no satisfactory theory of the changes that take place between the entrance of CO_2 into the plant and the production of carbohydrates.

Although deploring the lack of coordination among the various workers, and the tendency of botanists to accept without question the suggestions of physicists and chemists as to the nature of plant processes, the reviewers conclude that plant physiology is developing into an exact science, utilizing the experiences of the fundamental sciences, physics and chemistry, but having working principles and methods of its own. That it will thus be of great service in plant production requires no prophetic vision.—GEORGE B. RIGG.

Studies on oxidases.—In connection with his work on plant oxidases, BUNZELL[7] has published results of an investigation of the effect of hydrogen-ion concentration, C_h, on oxidase activity. Using his own simplified oxidase apparatus to measure oxidation and the gas chain to measure hydrogen-ion concentration, he finds that the oxidase activity of several kinds of material from potato tubers is completely inhibited by a C_h of $2.0\text{–}2.8\times10^{-4}$. The various concentrations were obtained by adding sodium hydroxide and acetic acid in various proportions, or either one alone, to mixtures of the plant material and pyrocatechin.

It is worth noting here that the two together constitute a true buffer solution capable of maintaining a fairly constant hydrogen-ion concentration, but that neither one alone suffices. Consequently, if there is a tendency for the acidity to increase in the Bunzell apparatus, as suggested by ROSE[8] in 1915, conditions are not comparable in the different mixtures. Those containing the true buffer solution will have practically a constant C_h throughout the course of the experiment, while those containing only sodium hydroxide or acetic acid will have a C_h which is larger at the end than at the beginning. The

[7] BUNZELL, H. H., The relationship existing between the oxidase activity of plant juices and their hydrogen-ion concentration, with a note on the cause of oxidase activity in plant tissue. Jour. Biol. Chem. **28**:315–333. 1916.

[8] ROSE, D. H., Oxidation in healthy and diseased apple bark. BOT. GAZ. **60**: 55–65. 1915.

latter condition holds true also for the controls, containing only water, pyrocatechin, and plant material. Furthermore, if the C_h changes during the experiment and only the initial concentration is determined, as in BUNZELL'S work, no very accurate conclusion can be drawn as to the effect of this factor on oxidase activity.

BUNZELL finds the inhibiting concentration for tulip tree material to lie between 1.58 and 5.02×10^{-3}, and for the magnolia between 3.5×10^{-3} and 8.91×10^{-4}. He considers that his results show "that the acid sensitiveness figure is a rather fixed number for any particular genus." He says also that it even seems "that the acid sensitiveness constant is the same or nearly the same for different genera (tulip and magnolia) of the same family (Magnoliaceae)." An analysis of his table III shows in general that the less the natural acidity of the plant material the lower the C_h necessary to cause total inhibition of its oxidase activity. This relation does not seem to hold in all cases, possibly because the various degrees of acidity used were too far apart to establish the inhibiting concentration with any great degree of accuracy.

If further work should prove such a relation general, new force will be added to the suggestions of BUNZELL and others that there is a distinct oxidase for each plant or group of closely related plants; not necessarily because they are protein in nature, however, as BUNZELL supposes. They may resemble each other in plants of the same family; they may show various properties of proteins, such as denaturing by acids, alcohol, and heat, and still be something quite different from proteins. BAYLISS suggests, on the basis of work by BACH and CHODAT and others, that oxidases are merely some form of iron copper or manganese kept in a disperse condition by various colloids. If these colloids are proteins the action of acids, for example, removes them as dispersing agents and allows the oxidases to precipitate. As a result of absorption, the two may come down together as a single precipitate which gives both protein and oxidase reactions without ever having existed as a real compound in the living plant. Such a hypothesis, however, fails to apply to peroxidases, for these, according to BEHRING, ASO, and BACH and CHODAT, are very little affected by heat. BACH and CHODAT also found that horseradish peroxidase when carefully purified contains no iron or manganese.

In connection with BUNZELL'S "acid sensitiveness figure," the question arises whether the inhibition he noted was all due to acidity. When a buffer solution of any sort is used to establish a definite hydrogen-ion concentration, elements are added which in the quantity used may be entirely foreign to the plant and productive of anomalous results. Illustrations of this are seen in BUNZELL'S table III. For example, extract of potato peeling with a natural C_h of 1.02×10^{-6} (no buffer solution being present) caused 22 per cent more oxidation than the same extract when a buffer solution was present and the C_h practically the same (1.04×10^{-6}). Even more marked are the results with potato sprouts, for with the C_h just about the same whether the buffer solution were present or not, they gave 16 per cent more oxidation without

it than with it. The data presented for "tulip tree leaves 1915" and "scaled tulip tree buds" show that when the solution in the oxidase apparatus had the natural reaction of the plant material, the oxidations were respectively 6.6 and 12 per cent greater than when the C_h, established by a buffer solution, was actually less than the natural C_h. In such a case it seems evident that some factor other than the hydrogen-ion concentration was effective as an inhibitor. The possibility that other ions play a part is indicated by work now being carried on by KRAYBILL and the writer.

The paper concludes with a brief review of the evidence, obtained by BUNZELL and others, of an increased oxidase activity in the leaf tissue in the case of physiological disturbances, and the possible meaning of such an increase. No mention, however, is made of work by ROSE on healthy and diseased apple bark in which it was shown that there is a much greater oxidase activity in the latter, correlated with a lower hydrogen-ion concentration.

REED,[9] in a paper published about the same time as BUNZELL'S, puts the inhibiting C_h for oxidase of potato extract at 5.5×10^{-4} (slightly higher than the $2.0-2.8\times10^{-4}$ found by BUNZELL), and for that of Red Astrachan apples at $5.0-7.0\times10^{-3}$. His statement that these concentrations are much lower than those given by previous investigators fails, however, to take account of BERTRAND'S report[10] in 1907, that a n/5000 solution of sulphuric acid ($C_h=5\times10^{-4}$) completely inhibited oxidation by sap of the lac tree. REED'S results would have meant more if he had measured oxidation by the BUNZELL apparatus rather than by the relatively inaccurate method of noting color changes, even though the BUNZELL apparatus, because of the poorly understood effects of hydrogen-ion and other inhibitors, leaves much to be desired in the way of accuracy.

One point is well made in this paper, namely, that plant extracts have an acid absorbing power which must cause inaccuracy in interpreting results obtained by adding buffer solutions to them if such results are not checked by careful determinations of the hydrogen-ion concentration. He found that when a given volume of 0.01 molar HCl was added to an equal volume of potato extract, the hydrogen-ion concentration, which should have been 5×10^{-3} if the potato extract acted like water, was actually only 5×10^{-4}. This decrease in acidity he thinks is due to proteins present in the extract as well as other amphoteric electrolytes, including probably phosphates and carbonates.

It is unfortunate, to say the least, that the authors of these papers have failed to cite adequately the literature pertinent to the phase of the subject with which they are dealing. Each has made a definite contribution to our

[9] REED, G. B., The relation of oxidase reactions to changes in hydrogen-ion concentration. Jour. Biol. Chem. **27**:299–303. 1916.

[10] BERTRAND, G., Bull Soc. Chim. France **1**:1120. 1907.

knowledge of the factors affecting oxidase activity, but the true value of this contribution would have been better shown by a fuller reference to other work.

KASTLE and BUCKNER[11] report experimental proof that phenolphthalein can be oxidized in the living plant. This they take to mean that free active oxygen is present in the tissues, apparently overlooking the possibility that combined oxygen might have caused the results observed. The reagent used, on oxidation, yields phenolphthalein, which is easily recognized by the pink color it gives with alkalies. When this test was applied to stalks of Indian corn which had been injected with the reagent, the pink color was found localized in the fibrovascular bundles of the stem and leaves. It was not found in the tassel, although lower down, close to the point of injection, there had been some diffusion into the cells adjoining the fibrovascular bundles. Similar results as to place of oxidation were obtained with okra.

The method here used offers a means of attacking the problem of oxidation in plants which should yield other valuable results if further developed and applied to a wider series of plants. It would be worth while to try whether phenolphthalein can be oxidized in the living plant when used in neutral or acid solution, and if so whether the oxidation is localized in particular cells or tissues. Such a test would allow for the effect of reaction (acidity or alkalinity), a factor known to be of great importance, not only in oxidation processes, but also in other processes carried on in living tissues. The effect of reaction might also be studied in acid fruits and in tissues affected by "physiological diseases" or by diseases due to bacterial or fungus parasites. In several cases such tissues have been found to be less acid than healthy ones, but little is known concerning variations in reaction within the tissues themselves.—D. H. ROSE.

Experiments in girdling.—A contribution by HIBINO[12] is of interest both to plant physiologists and horticulturists, since it will aid in furnishing a more definite chemical basis for the interpretation of the behavior of girdled plants. In the past there has been no lack of references to the accumulation of elaborated foods above the girdles; it is certainly worth while to have some definite determinations of these compounds and their relative quantities.

Five types of girdling were tried on *Cornus contraversa* Hemsl. These consisted in (1) removing a complete ring of bark, (2) removing a complete ring of bark and some of the wood, (3) removing half a ring of bark, (4) removing half a ring of bark and wood, and (5) boring completely through the wood. The wounds were left unprotected. The last three methods of treating the material resulted in responses similar to the untreated controls in nearly all cases.

The general external results noted are those commonly recorded in girdling experiments. The main interest of the present paper centers in the presenta-

[11] KASTLE, J. H., and BUCKNER, G. DAVIS, Evidence of the action of oxidases within the living plant. Jour. Amer. Chem. Soc. **39**:479–482. 1916.

[12] HIBINO, SHIN-ICHI, Effekt der Ringelung auf die Stoffwanderung bei *Cornus controversa* Hemsl. Jour. Coll. Sci. Imp. Univ. Tokyo **39**:1–40. *pls. 1, 2.* 1917.

tion of material which may aid in an explanation of the cause of these conditions. Unfortunately the experiments are limited and the analyses of the nitrogenous compounds are not sufficiently complete to furnish any sort of basis for judging what rôle they may play. The data on the carbohydrates, however, are of considerable interest. In studying the effects of girdling on nutrition in general, at least three of the many points concerned in growth must be considered: (1) a possible modification of the intake of nutrients by the roots; (2) the synthesis of products from these compounds and those resulting from photosynthetic activity; and (3) whether these compounds are stored or utilized. We are given some light on the third point only. It is a fair question to ask whether the ability of the roots to take up salts is not as profoundly modified by the character and quantity of the organic nutrients in the parts above ground and with which such salts may be combined, as it is by the so-called starvation effects brought about by cutting off the supply of organic nutrients from the tops to the roots. Girdling could bring about both of these situations. The question arises as to why the carbohydrates accumulate above the girdles. As commonly stated, this may be due to the fact that these products are held from passing into the roots. There is little evidence which would show that it may not also be due to a deficiency of mineral nutrients, particularly nitrates, to aid in their utilization in forming other compounds or growth. A study of the ratios of carbohydrates to moisture, nitrogenous compounds, and other mineral nutrients in their relation to the entire phenomenon of growth is greatly to be desired. While this situation is not dealt with by HIBINO, his results and those of several previous investigators furnish ample encouragement to warrant investigation.

The increase in anthocyanin accompanying an increase in reducing sugar confirms the findings of previous workers with other plants. The yellowing of the foliage above a girdle is a usual condition. That this should accompany an increase in carbohydrates is interesting. It is unfortunate that no analyses of the nitrogenous compounds in the leaves are available. Lacking such determinations nothing can be said concerning their possible relationship to the carbohydrate situation, nor the moisture situation. The fact that the percentage of moisture in the leaves is lower when carbohydrates form a higher percentage of the weight might be expected when the moisture holding capacity of these compounds is considered.

The single quantitative determination of the reserve materials in the twigs in midwinter is not sufficient for any general conclusions. Again, it is unfortunate that all the nitrogen is computed as protein. It is more than likely that all of it is not, and quite probable that the several forms of nitrogen may exist in different proportions in the several lots examined. A quantitative analysis at the time of active vegetation would have been even more significant regarding the influence of the several substances on growth. Striking as are the differences in the several lots, the results cannot be interpreted with certainty unless compared with figures for similar parts at several periods during the

year. Whether the differences shown by the bark and wood girdled material may be accounted for by a decreased moisture supply in the latter is an open question. It is interesting to note, however, that many plants grown with a deficiency of water do show an increased tannin content.

While it is impossible to draw broad conclusions from the results presented, the work constitutes a genuine contribution toward a more nearly complete knowledge of the causes of the responses following girdling, and adds to the available information on the entire problem of growth. In any future work it would be particularly desirable to follow the nitrogenous compounds and mineral nutrients as well as the carbohydrates, more especially with a view toward the determination of the ratios of these various substances in relation to the observed responses.—E. J. KRAUS.

Imbibition.—MACDOUGAL[13] and MACDOUGAL and SPOEHR[14] are doing work on the effects of acids and bases on imbibition of water by plant tissues and plant gels that promises to be the most significant contribution in this phase of plant physiology that has been made for some decades. Practically all of the work on the effect of acids and bases on the amount of swelling and force of swelling of gels and on the viscosity and osmotic pressure of sols has been done on the amphoteric protein gels. For these it seems well established that the iso-electric point (the reaction at which the particles are without a charge) is the point of minimum swelling, force of swelling, osmotic pressure, and viscosity, and that forcing the ionization of the gel or sol either to the positive by addition of an acid or to the negative by the addition of a base increases the swelling, osmotic pressure, and viscosity very markedly.[15]

MACDOUGAL and SPOEHR find that both base and acid additions (n 0.01) decrease greatly the swelling of agar plates and to a less degree of *Opuntia* tissue. In fact, *Opuntia* tissue acts more like mixtures of gelatine and agar than it does like either gelatine or agar. These results suggest that in contrast to the protein gels and sols, the point of maximum swelling, viscosity, etc., in agar is the iso-electric point and that the positive agar due to acid addition or the negative agar due to base addition shows a lowering of these characters. In this connection it is to be regretted that the H^+ concentration for the iso-electric point of agar has not been determined. It is also desirable to know the behavior of various other carbohydrate gels and sols (mucilages, pectic materials, gums, etc.) to see whether this contrast in behavior is a general difference between the protein and carbohydrate gels. It seems that plant physiologists have generally assumed that the laws of behavior of protein

[13] MACDOUGAL, D. T., Imbibitional swelling of plants and colloidal mixtures. Science **44**:502–505. 1916.

[14] MACDOUGAL, D. T., and SPOEHR, H. A., The behavior of certain gels useful in the interpretation of the action of plants. Science **45**:484–488. 1917.

[15] HOBER, R., Physik. Chemie Zelle Gewebe. 329–338. 1914.

colloids hold for all hydrophilous colloids with which they have to deal, protein as well as carbohydrate. This work seems to make evident the error of such a general assumption.

A quotation from the last paper gives the author's view of the physiological significance of these results. "The general identity of constitution of these colloidal mixtures and of cell-masses, and the obvious similarity of their behavior, together with newly determined features of carbohydrate metabolism not described in this paper, make it possible to correlate more closely the processes of imbibition, metabolism, and growth, and on the bases of these interrelations, to interpret growth enlargement and incidental variations in volume and size of organs." No doubt many will differ from a statement in another part of the paper that amorphous carbohydrates form a very important part of the plant protoplast. There seems little evidence that amorphous carbohydrates (excepting starch, which would have no bearing here) are general constituents of the plant protoplast. When amorphous carbohydrates are constituents of the protoplast they generally appear as discrete particles of micronic size and not in intimate mixtures with proteins and distributed in particles of submicronic or amicronic size, as must have been the case in the agar gelatine mixtures with which the authors worked. Of late we are coming to know that amorphous carbohydrates of the walls and intercellular spaces have considerable physiological controlling action. This is especially true in seeds. This work is very suggestive in this connection also.

This work may have a very important bearing on the daily transpiring power of certain of the cacti as found by various workers in the Desert Laboratory. In these there is apparently no stomatal regulation, and the lowest transpiring power is during the day. This corresponds to the daily change in acidity. The time of low transpiring power is the time of low acidity, when, according to the findings of MACDOUGAL and SPOEHR, the gels of the tissues will have the greatest power to take up and hold water. With this no doubt there will be a rise in viscosity. These physical conditions will all tend to lower the rate of movement of water toward the intercellular spaces and to lower the vapor pressure within those spaces. This in turn will lower the rate of outward diffusion. This suggested relation needs careful investigation. On the basis of the behavior of protein gels the daily variation in the transpiring power of the cacti was not intelligible. This work should be a great stimulus to much work along similar lines.—WM. CROCKER.

Taxonomic notes.—BRITTON,[16] in continuing his studies of West Indian plants, has described new species in *Cleome*, *Chamaecrista* (3), *Leucocroton* (3), *Passiflora* (3), *Rondeletia* (10), *Eriocaulon* (3), *Dupatya*, *Pilea*, *Ichthyomethia*,

[16] BRITTON, N. L., Studies of West Indian plants. IX. Bull. Torr. Bot. Club 44:1–37. 1917.

Castelaria, and *Stenostomum* (2). There is a synopsis of the species of *Chamaecrista* in the West Indies (31 spp.); of the Cuban genus *Leucocroton* (7 spp.); of *Passiflora* in Cuba (21 spp.); and of *Rondeletia* in Cuba (35 spp.).

DECANDOLLE,[17] in a study of specimens of Meliaceae from Central America and Panama sent by the United States National Museum, has described 9 new species in *Guarea* and 2 in *Trichilia*.

HEDGCOCK and HUNT[18] have described 5 new species of *Peridermium* on pine needles in the eastern United States.

KERN,[19] in a monograph of the North American "sedge rusts," recognizes 19 species of *Puccinia*, 3 of which are described as new.

PENNELL,[20] in continuing his studies of our southern plants, has presented the genus *Chamaecrista* as represented in the United States. He recognizes 13 species, which include 3 new species and 2 new combinations.

WAGER[21] has published a list of the mosses of South Africa, which for the first time brings together all the known mosses of South Africa. The list includes 846 species in 160 genera, representing 37 families. The names of 27 new species, representing 23 genera, are also included, one of the genera (*Physcomitrellopsis*) being new. These will be described and published later.

WILLIAMS,[22] in reporting the mosses obtained on a collecting trip in the Philippine Islands, extending from October 1903 to August 1905, lists 240 species in 118 genera. Of these, 27 species and 3 genera (*Rhabdoweisiella*, *Pseudopohlia*, *Stereodontopsis*) are described as new.—J. M. C.

Endosperm color in maize.—In crosses between California Golden Pop maize and a white endosperm variety obtained from HAAGE and SCHMIDT under the name *Zea Caragua*, WHITE[23] finds white dominant. These results are interpreted by assuming the presence of an endosperm suppression factor *A* in the *Zea Caragua* in addition to the usual color factor *y*. This new primary factor affecting endosperm color raises the number of such factors to three; in addition there are numerous secondary factors.—E. M. EAST.

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